

# MISSOURI Natural Areas NEWSLETTER

2023  
Volume 23, Number 1

"...identifying, designating, managing and restoring the best remaining examples of natural communities and geological sites encompassing the full spectrum of Missouri's natural heritage"

## Editor's Note

# Threats to and Viability of Missouri's Natural Areas

In recent years, the concept of maintaining ecosystem resilience in an altered natural world has taken on greater significance in light of rapid environmental change. Efforts to improve biodiversity resilience in natural communities surrounded by urban and agricultural development and the ensuing disruption of ecological processes requires thoughtful, careful planning and implementation. One of the core concepts of resiliency of natural spaces involves size; larger natural zones tend to allow for greater ecosystem function (Beller, et al. 2019).

For the past 25 years or more, the Missouri Natural Areas Committee has embraced the concept that resilient ecosystems often require large-scale zones with buffer areas of similar landscape types. In recent years, for example, following a long history of restoration, the committee approved the expansion of the Coakley Hollow Fen NA from 5 acres to 1,773 acres to include the surrounding diverse woodlands and fens. Small, though intact high quality natural communities including small patches of railroad remnant prairies or sinkhole ponds, have great value in protecting and preserving biodiversity. However, they come with their own significant external threats. In the case of the railroad remnant prairies, one fast swipe of roadside herbicide can cause them to wink out forever.



Photo by Allison Vaughn, Missouri Department of Natural Resources

**Image 1.** Lincoln Hills Natural Area (1,872 acres) in Cuivre River State Park (MDNR, 6,400 ac.) encompasses a smaller natural area, Pickerelweed Pond, a small sinkhole pond natural area designated in the 1980s. The natural area surrounding Pickerelweed Pond expanded in 1998 to include the frequently burned and managed surrounding woodlands. Deer and exotic species management have occurred in the natural area and throughout the park for over 35 years. Urban encroachment at the park's borders remains a viable threat, and staff work assiduously to continue management of this landscape-scale natural area.

This issue of the Natural Areas Newsletter focuses on not only threats to the viability of natural areas, but also the resiliency inherent in stable, intact ecosystems. In this issue, the complex story of Pershing State Park (5,257 acres) is detailed as this isolated natural system continues to be under significant threat from the external forces of the surrounding landscape. In a rare event, we republished an article with permission from the *Journal of Applied Ecology* regarding the destabilizing nature of deer overpopulation in forested systems; deer overbrowse remains a particular threat to our urban, isolated Missouri natural areas. Read on about a lesson in resiliency of a stable karst natural area following the 9 years long mitigation process to undo the result of long tenured external threats.

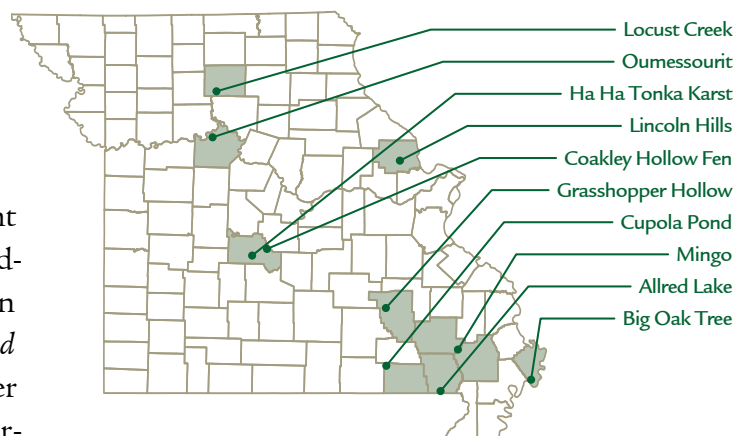
Significant efforts continue to occur in Missouri as a means of rebounding from not only extreme events, but also press disturbance, the long-lasting disturbance that if not mitigated can permanently alter an ecosystem. Missouri natural areas remain among the best of type natural communities and geologic features, and land managing agencies and private landowners take pride in their efforts to restore, maintain and preserve these special areas. Read on to learn more about restoration efforts in natural areas, and some of our most pressing threats to viability. Author contact information is listed at the end of each article, so feel free to reach out with questions or for further discussions.

— Allison J. Vaughn, editor 🍃

Allison J. Vaughn is a Natural Resource ecologist with the Missouri Department of Natural Resources.

Contact: [allison.vaughn@dnr.mo.gov](mailto:allison.vaughn@dnr.mo.gov)

## NATURAL AREAS FEATURED IN THIS ISSUE



## CONTENTS

Threats to and Viability of Missouri's Natural Areas	
Allison Vaughn.....	1
Building a Lasting Natural Heritage Legacy for Missouri Wetlands	
Kelly Srigley Werner .....	3
Conservation of Mead's Milkweed in Missouri: New Insights, Persistent Struggles, and Ongoing Research That Guide Future Conservation Efforts	
Malissa Briggler.....	9
A Prairie Persists: A Tale of Resilience and Loss in a Wet Prairie System	
Carrie Stephen.....	14
Where Will Midwest Ecosystems Be in 2500?	
Adam B. Smith .....	22
The Persistent Threats of Dominance & Hierarchy	
Justin Thomas .....	28
The Long-Term Impacts of Deer Herbivory in Determining Temperate Forest Stand and Canopy Structural Complexity	
Samuel P. Reed, et al.....	32
Woodland Restoration Truly Benefiting Birds in Missouri	
Frank R. Thompson.....	44
A Long Lesson in Resiliency: Ha Ha Tonka Karst Natural Area	
Allison J. Vaughn .....	48

## NATURAL AREA NEWS

In Memoriam: Nels Holmberg.....	27
Calendar of Events.....	47

The *Missouri Natural Areas Newsletter* is an annual journal published by the Missouri Natural Areas Committee, whose mission is identifying, designating, managing and restoring the best remaining examples of natural communities and geological sites encompassing the full spectrum of Missouri's natural heritage. The Missouri Natural Areas Committee consists of the Missouri Department of Natural Resources, the Missouri Department of Conservation, the U.S. Forest Service, the U.S. Fish and Wildlife Service, the National Park Service and the Nature Conservancy.







**Image 1.** Duck hunters often see the splendor and beauty of wetland habitats at sunrise. Here the sun is rising over an emergent marsh in winter.

## Building a Lasting Natural Heritage Legacy for Missouri Wetlands

by Kelly Srigley Werner

Every year, World Wetlands Day falls on February 2 and in 2023, a cadre of over 300 conservation professionals, educators and landowners met February 1–3 at the Lake of the Ozarks for a Missouri Wetland Summit, co-hosted by the Conservation Federation of Missouri and the Missouri Department of Conservation. The summit was designed to reignite a commitment to conserving, restoring and protecting wetland habitats for the health of the land, water, wildlife and people.

A recurring theme from the presenters at the conference was that science must be a cornerstone in wetland conservation because of the vital role all wetlands play in ensuring clean and healthy water for all who depend on them. At the conclusion of the summit, the excitement was palpable and a flurry of ideas and sugges-

tions were offered from over 300 attendees. But, shortly after the summit, the nation learned that the Supreme Court of the United States handed down a decision that erased decades of protections for wetlands under the Clean Water Act. The ruling states that only those wetlands that are connected to surface water flow will be recognized for federal protections under the Clean Water Act. This is concerning, not only for Missouri, but for states that have numerous isolated wetland habitats like the prairie pot-holes in the Dakotas and upper Midwest.

Can Missouri's commitment to wetland conservation keep pace with the implications of this ruling? If you are a proponent of diverse landscapes that support diverse fish and wildlife resources, contextualizing Missouri wetlands and the various niches they fulfill is as import-

ant as knowing the historical extent of wetlands and the related social and economic changes that have occurred over time.

### Missouri Wetland Status and Trends

Missouri's land base is about 44.6 million acres. Although not yet a state, the U.S. Fish and Wildlife Service estimated that around the time of the American Revolution (1770s) there were approximately 4.84 million acres of wetlands, about 10.9% of the state's surface area. Nearly half of that acreage (2.3 million acres) occurred in the Missouri 'bootheel' and was dominated by expansive bottomland hardwood forests and cypress-tupelo swamps. The other half were various complexes of wet prairie and emergent

wetlands, bottomland hardwood forests and scrub-shrub wetland habitats occurring along our large rivers and streams and those associated with karst systems (Figure 1).

By 1980, the wetland base acres had been reduced from 4.84 million acres to roughly 643,000 acres, or about 1.4% of the surface area of the state. So, approximately 87% of the original wetland acres in Missouri were lost by 1980. This was all progressive, the reduction of wetland acreage required societal 'progress' for around 200 years to channelize rivers, construct dams, ditch, tile, fill and constrict wetland water flow with elaborate levee systems; essentially removing the processes that originally and naturally shaped and created wetland habitat.

**Figure 1.** Historical reference where the largest concentrations of wetlands were located on the landscape exhibited by hydric soils.



Mike Leahy/ Missouri Department of Conservation

Other states in the Midwest, and nationwide, also experienced extensive wetland loss during this time period, and for people along the rivers, the Mississippi and Missouri rivers, wide-ranging wetland loss occurred in the lands between the bluffs. Between 2004 and 2009, both emergent marshes and forested wetlands continued to decline nationally (0.2% and 1.2% respectively) as well as in Missouri. But throughout that earlier timeframe, wetlands were not understood in the same way they are now, and the science continues to evolve even today.

---

### Irreplaceable Biological and Ecological Values

---

Missouri wetlands play a critical role to birds during spring and fall migration including species of waterfowl, shorebirds, large wading birds, secretive marsh birds, songbirds and raptors. As part of the Mississippi Flyway, millions of birds hone in on Missouri for a place to rest and refuel due to the mid-latitude location of the state along migratory routes.

The diverse array of wetland types and habitats provided in Missouri can't be overstated. It is this diversity in wetland types that makes Missouri wetlands support a plethora of niche species too, such as insects, butterflies, amphibians, reptiles, mammals, fish, and plants. Wetlands provide much needed refuge for species of conservation concern like three-toed amphiuma, swamp rabbit, and prairie massasauga rattlesnake, monarch butterfly and federally-listed species like Hine's emerald dragonfly, pondberry and decurrent false aster.

Most of Missouri wetlands occur along rivers and streams as marshes, swamps, sloughs, oxbows and forested wetlands, and some more obscure wetlands occur deep in the Ozarks as seeps, fens and sinkhole ponds.

Over time, science has informed us that ecologically, wetlands provide flood control, absorb

nutrients (reduce nitrogen and phosphorus in streams) and pollutants from runoff, reduce erosion and sedimentation in streams, recharge groundwater, sequester carbon in a changing climate, provide recreation and social interactions through hunting, wildlife watching and outdoor learning. These values are important for people and wetlands, as part of a healthy ecosystem, and help maintain healthy, clean water, and provide a valuable connection to water supplies.

So, with these values in mind, it is more important than ever to think of wetlands holistically with an ecosystem approach to conservation which must include the human dimensions element in decision-making, striving for open communication concerning knowledge of status and trends, ecological importance, and critical benefits that wetlands provide to our citizenry and our state's natural heritage.

---

### A Closer Look into the Supreme Court Decision

---

Today, it is difficult to comprehend the impacts to the processes that conserved and protected wetlands over generations. But in the 1970s, because wetland losses were not just occurring in Missouri, national legislation was passed to stop the continued losses, recognizing among other things the science related to wetlands' role in flood storage and ground water recharge.

Wetlands have been protected for over 50 years and are considered waters of the United States under the Clean Water Act of 1972. Through a regulatory process under Section 404 of the Clean Water Act, wetlands require permits before any dredging or filling, and mitigation of impacts are required to replace the acres impacted if there are no other alternatives. In addition, a presidential Executive Order 11990 beginning in the late 1970s and carried through administrations on both sides of the aisle declared a no net loss of wetlands: 1) due to their important



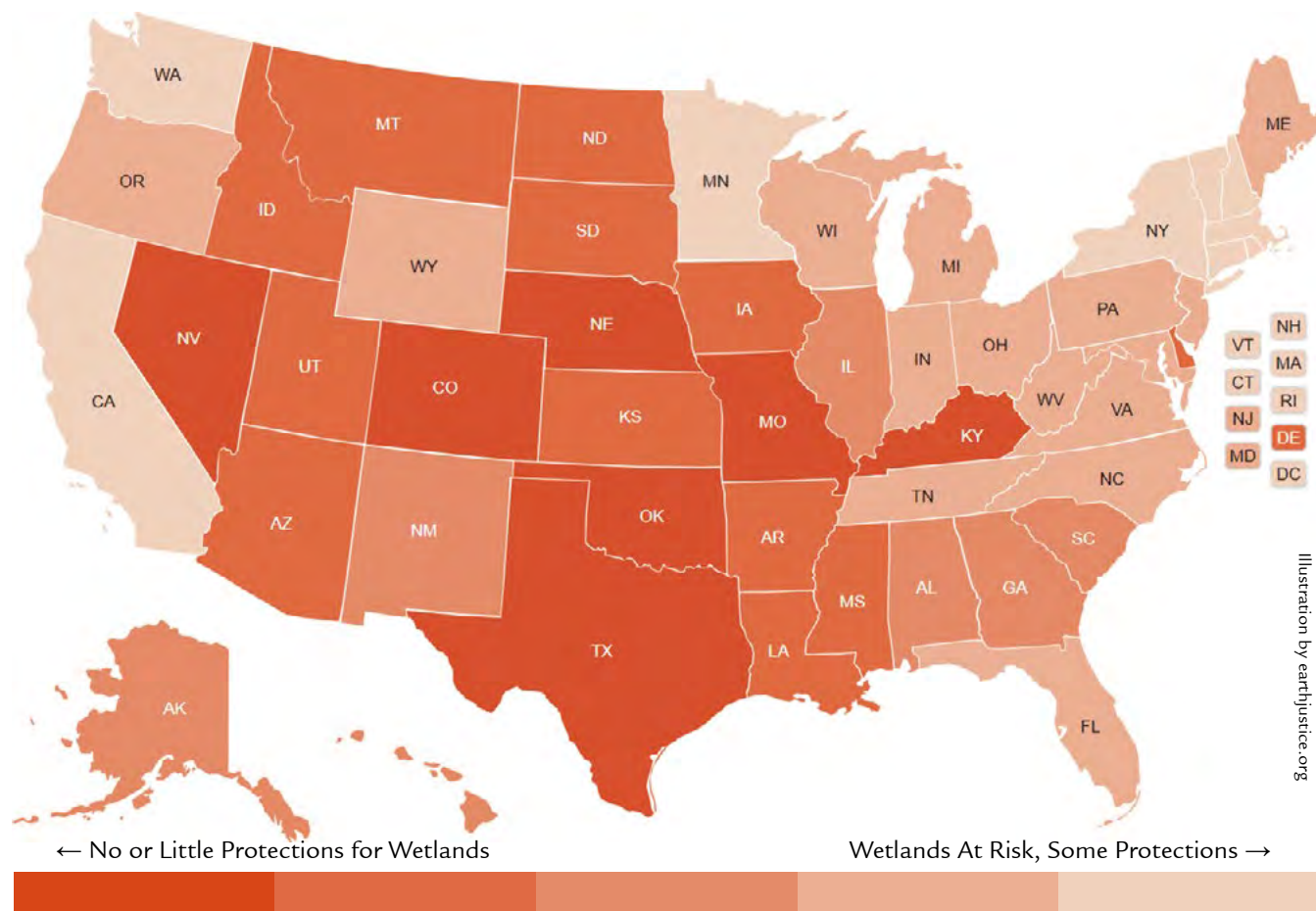
roles in protecting public health, safety and welfare; 2) supporting flora and fauna in natural systems, and; 3) other uses such as recreation, and cultural and scientific study. Societal tests of the definition of a wetland and whether they should be considered waters of the U.S. regulated under the Clean Water Act have been challenged in court over the last several decades.

The spring 2023 split (5-4) Supreme Court decision to limit the definition of a wetland under the Clean Water Act did not take into account Justice Kennedy's language in previous challenges regarding the application of science in determining jurisdiction, putting the bulk of the nation's remaining wetlands at risk.

In Missouri, the Clean Water Act, through section 401 gives states authority to protect wetlands from certain activities through their state water quality certification program. But that authority in Missouri is directly tied to the Clean Water Act's section 404 permit process at the national level. Meaning that if a 404 permit is not required, nor is a 401 certification.

This decision could potentially impact over half of the remaining wetland acres in the United States including the acres left in Missouri for a few reasons: 1) the state has few alternative laws for protections in place (Figure 2); 2) many wetlands, while connected to a river or stream are cut off from surface flow due to levees; and 3) fens and seeps are connected to ground water

**Figure 2.** Missouri is one of 7 states where wetlands are most at risk after the Supreme Court decision to limit the definition of wetlands to only include those with direct surface flow to a water of the U.S.



that ebbs and flows, without a discernible surface source, rendering important habitats like these, sinkhole ponds and wetlands near losing streams, to have no protections. Put another way, the 13% of wetlands that remain could be reduced to 6.5% or less than 1% of the state's land base.

---

### Partnership Efforts and a Call to Action for Missouri Wetlands

---

Missourians are strong advocates for natural resources and over the years have voluntarily stepped up to the plate to invest in conservation through support for the "Design for Conservation" which provided 1/8 of a cent sales tax to directly support forest, fish and wildlife management.

State and federal agencies and organizations have worked together in partnership and with voluntary landowners and communities to protect and restore wetland habitats and educate people on their management. While unrealistic to imagine Missouri's land base being restored to 10.9% of its original wetland base, landowners voluntary conservation actions have resulted in positive collaborations through various public-private partnerships on private lands including in north-central Missouri, the bootheel, and the Missouri-Mississippi River Confluence.

Missourians engaging in efforts to work with the U.S. Fish and Wildlife Service's Partners for Fish and Wildlife Program, Ducks Unlimited, Inc's Land Protection Program, Missouri Department of Conservation's Landowner Assistance Program and the Natural Resources Conservation Service's Wetland Reserve Enhancement (WRE) Program and other private organizations have helped to restore approximately 200,000 (WRE around 166,000 acres) acres providing some gains of wetland habitat over the last 35 years — a significant investment in time and money but also a local economic driver to contract the work and provide materials for construction.

Efforts can't stop here though. "For 50 years the Clean Water Act has been instrumental in revitalizing and safeguarding drinking water sources for people and wildlife, wetlands for flood control, and habitats that sustain our wildlife heritage," said Jim Murphy, director of legal advocacy for the National Wildlife Federation. "We call on both Congress and state governments to step in, plug the gap, and protect our threatened waters and the people that depend on them."

We need social connections with Missouri wetlands to generate renewed support with our local communities and citizenry. Our Missouri Natural Areas Program celebrates the variety of wetland habitats in our state by protecting and recognizing 51 natural areas with wetlands as the primary feature, including the following community types and a few examples: Wet Bottomland Forest (Big Oak Tree NA), Wet Bottomland Prairie, Marsh (Oumessourit NA), Shrub Swamp (Mingo NA), Swamp (Allred Lake NA), Oxbow & Slough, Sinkhole Pond Wetlands (Cupola Pond NA), Fens and Seeps (Grasshopper Hollow NA). Each natural area wetland represents many irreplaceable biological and ecological values.

To answer the question early on in this article, "Can Missouri's commitment to wetland conservation keep pace with the implications of the Supreme Court ruling?" The answer is yes, but it will require strong leadership and local partnerships, perhaps focused on Missouri's many designated natural areas with a wetland focus, to generate appreciation. This can be done through local events like workshops and festivals that can, in turn, change hearts and minds about how wetlands affect people's everyday lives and why wetlands need strong advocacy, policies and protections. Other ideas include holding a State Wetlands Day, where communities celebrate Missouri wetlands perhaps in combination with birding festivals and soil health demonstrations.

Wetlands are a part of the patchwork of our state's natural heritage and while the court's decision is troubling, citizens have a voice and can build support serving as messengers and ambassadors for wetlands. Take friends to a wetland to let them 'touch' the resource and get their feet wet. Building that advocacy is a first good step in leaving a lasting wetland legacy for future generations of Missourians. 🌿

---

**Kelly Srigley Werner** retired from a 34-year career with the U.S. Fish and Wildlife Service in 2021, where for 28 years she served as the Missouri State Private Lands Coordinator and Administrator for the Partners for Fish and Wildlife Program.

Contact: [srigleywerner@uidaho.edu](mailto:srigleywerner@uidaho.edu)

#### References

**Dahl, T.E.** 1990. "Wetland Losses in the United States 1780s to 1980." U.S. Department of Interior, Fish and Wildlife Service, Washington D.C. 13 pp.

**Dahl, T.E.** 2011. "Status and Trends of Wetlands in the Conterminous United States 2004 to 2009." U.S. Department of the Interior; Fish and Wildlife Service, Washington, D.C. 108 pp.

"Section 401 Water Quality Certification: Protecting Missouri's Wetlands—PUB2151." Missouri Department of Natural Resources Water Protection Fact Sheet

**Supreme Court of the United States.** "Syllabus, Sackett et ux. v. Environmental Protection Agency et al. Certiorari to the United States Court of Appeals for the Ninth Circuit. No. 21-454." Argued October 3, 2022—Decided May 25, 2023

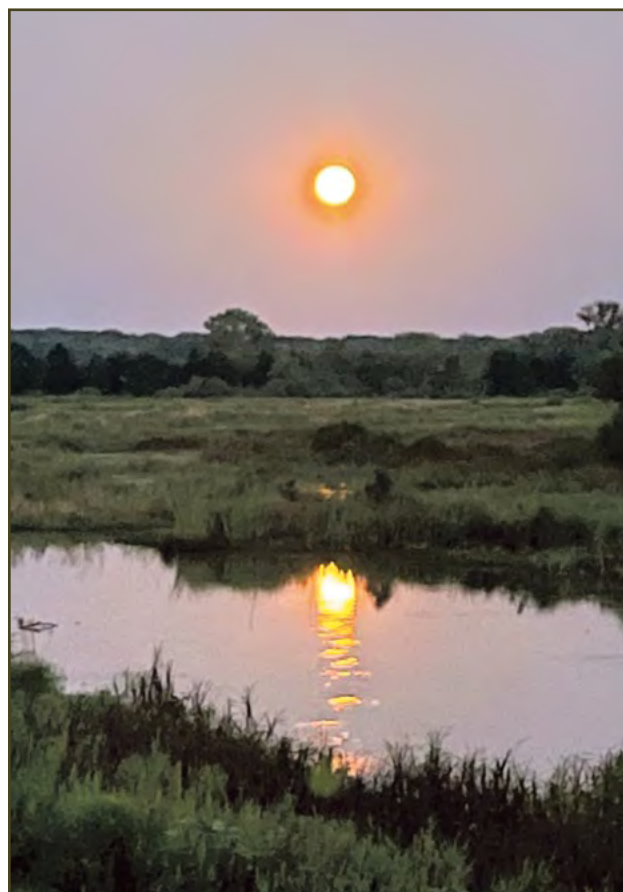


Photo by George Seek

**Image 2.** North-central wet prairie marsh captured under a blue moon September 2023

**MISSOURI NATIVE  
GRASSLANDS**  
*Summit 2024*

**April 9-11, 2024**  
Capitol Plaza Hotel  
Jefferson City, Missouri

Attendance will be limited. Early  
registration begins in December 2023.

**Register at**  
[confedmo.org/grasslands](https://confedmo.org/grasslands)



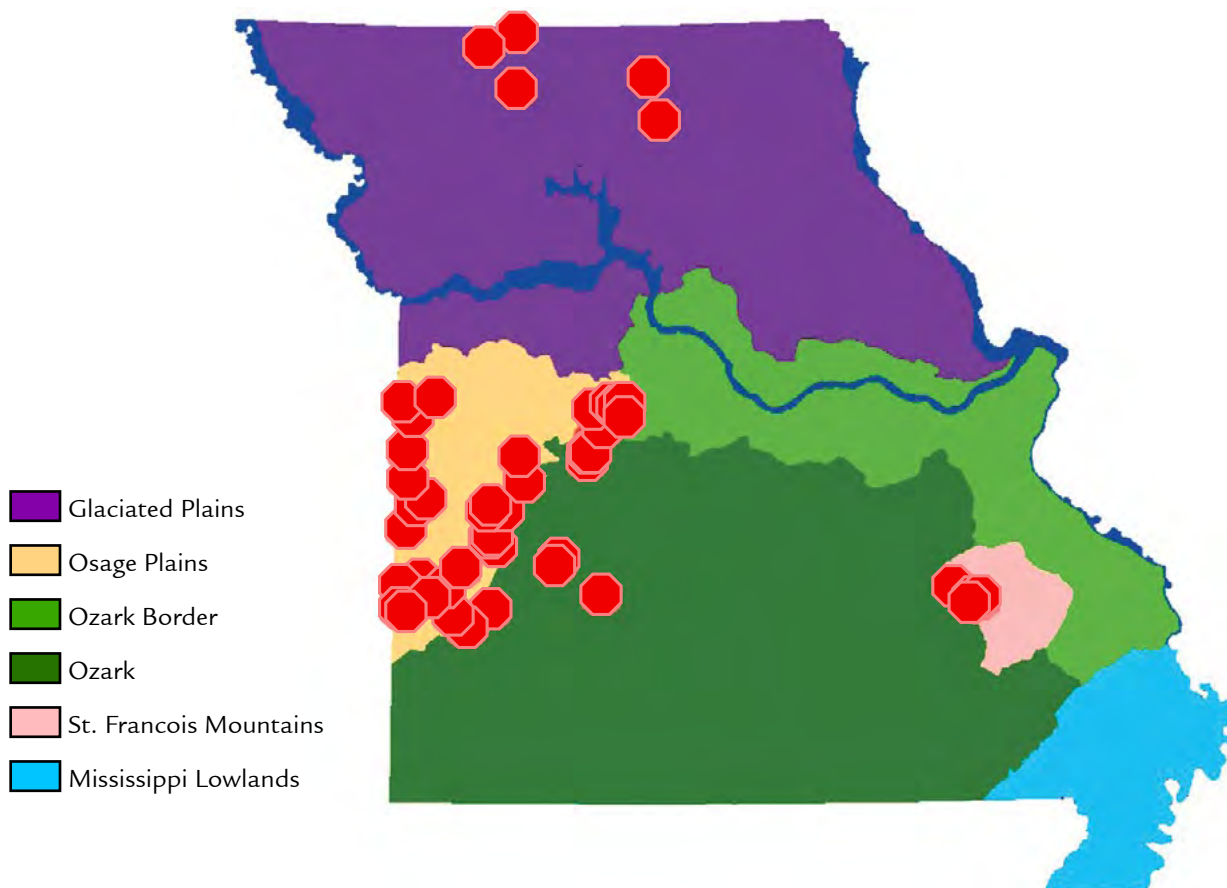
# Conservation of Mead's Milkweed in Missouri: New Insights, Persistent Struggles, and Ongoing Research That Guide Future Conservation Efforts

by Malissa Briggler

Mead's milkweed (*Asclepias meadii*) is a long-lived perennial currently found on tallgrass prairie remnants in Kansas, Missouri, Illinois, and Iowa, in addition to igneous glades of the St. Francois Mountains of Missouri (Figure 1). Unlike in the Glaciated Till Plains of the northern tallgrass prairie region, in southern Missouri tallgrass prairie, conversion to crop production was low because these regions were characterized by rocky and less productive soil. Missouri's most valuable and intact prairie systems that include populations

of Mead's milkweed primarily exist in the Osage Plains Region located in the west-central and southwest portions of the state. Igneous glades within the St. Francois Mountains of the Missouri Ozarks also harbor populations of Mead's milkweed. These populations are isolated in a geographically small landscape, but appear to be faring better in regards to abundance and seed production than those existing in the Osage Plains Region. Mead's milkweed populations have declined with the overwhelming loss of tallgrass prairie and struggle even in

**Figure 1.** Distribution of Mead's milkweed populations currently tracked in the Natural Heritage Database.



Credit Malissa Briggler



**Image 1.** Mead's milkweed and other vegetation uprooted and destroyed by feral hogs in the St. Francois Mountains.

protected, high-quality remnants. The species is currently listed as federally threatened and state endangered in Missouri.

Monitoring of Mead's milkweed populations occurs on state, federal, and privately owned land, as well as property owned by non-government organizations. The frequency and intensity of monitoring programs vary greatly. Some populations are monitored by counting stems every 3–5 years while other monitoring efforts involve long-term, permanently marked locations where each individual plant is mapped. Intensive monitoring on designated natural areas has remained a priority over the past thirty years. The Missouri Natural Heritage Program maintains the monitoring data in order that it can be integrated for strategic land management, conservation planning, and protection of the species. Currently, 65 populations tracked in the heritage database are occasionally or frequently monitored.

Monitoring data have provided valuable information to better understand and predict responses of Mead's milkweed to management. Mead's milkweed responds well to late season or dormant season burning. It also persists well under a frequent haying regime that more commonly occurs on private land. Populations of Mead's milkweed that are periodically burned or hayed have shown to be stable over the past two decades. A substantial and sustained reduction in stem counts has been seen in areas where fire and/or haying have ceased or undergone extensive periods (>5 years) of rest. A return of burning or haying can reverse this trend and increase stem counts, but consistent application over time is generally required.

Some populations of Mead's milkweed have undergone extensive damage by feral hogs (Image 1). While feral hogs are present in the Osage Plains Region, populations are greater in the





**Image 2.** A Mead's milkweed flower possibly pollinated with the help of a Brown-belted bumblebee (*Bombus griseocollis*.)

rugged terrain of the St. Francois Mountains, including the igneous glades containing populations of Mead's milkweed. Hog damage control on federal, state, and private lands include trapping, aerial gunning as well as electric fencing to deter hogs from entering glades with the best populations of Mead's milkweed. These efforts are instrumental to protecting populations from severe damage. Control efforts are making significant progress on feral hog eradication, but feral hogs remain a known threat in the region.

Another alarming trend occurring over the past twenty years is a lack of seed production. Some populations have produced over a hundred flowering stems with few, if any, developing a viable seedpod. Mead's milkweed can only pol-

linate and produce viable seedpods by cross pollinating with another genetically distinct individual (Image 2). This phenomenon is called obligate outcrossing. Historically, many of the native prairie remnants that support Mead's milkweed were managed by frequent or even annual haying. Biologists theorized that frequent haying of Mead's milkweed may have led to greater vegetative growth as plants were consistently harvested before seed production. Over time, the individual plants began producing more stems along their rhizomes, which are called ramets as they are not genetically distinct individuals. These multiple stemmed plants, though numerous, are unable to cross-pollinate, which is needed to produce genetically distinct individuals known as genets. It is theorized that



the lack of seed production is due to these large populations consisting of mostly ramets and not genets. Working with this assumption, some recovery actions included transplanting efforts to boost genetic diversity.

However, biologists are also concerned that transplanting individuals across populations may decrease the genetic integrity of Mead's milkweed. The concept that a lack of genetic diversity results in low seed production was just a theory and there was concern that introducing plants from one population to another population across a great distance, or from a different prairie/glade habitat, could exacerbate a genetic decline instead of remove it. A phenomenon known as outbreeding depression can occur when two genetically distant groups that are adapted to different environmental conditions cross and produce offspring with reduced fitness. Thus, transplanting to stable populations was delayed until research determined whether outbreeding depression would be a possible consequence. In the meantime, transplanting efforts continued on native prairie containing just a few stems or at sites that had historic, but not extant, populations of Mead's milkweed.

Since 2011, biologists have planted over 700 Mead's milkweed seedlings throughout the tall-grass prairie range in Missouri. Eight sites were selected based on three criteria: suitable habitat, having a management plan for those lands that included burning or haying at least once every 3 years, and the proximity to only a few remnant plants or historic locations of Mead's milkweed. Twenty to thirty percent of seedlings have persisted at sites planted 13 years ago. Data also show that stems remain dormant on occasion. Between 2011 and 2017, 600 transplants were monitored each year. Presence data was collected at each transplant location. Observations of extended periods of dormancy were recorded as plants remained dormant for 1 or more years,



Photo by Emily Homer

**Image 3.** Wind-dispersed seed of Mead's milkweed waiting for the next breeze.

followed by a year that the plant produced a stem. These observations remain important for better understanding the life history characteristics of Mead's milkweed and to gather reasonable expectations from translocation efforts.

In 2018, Dr. Christine Edwards with the Missouri Botanical Garden began investigating genetic diversity and genotypic richness within and among 12 Mead's milkweed populations in Kansas and Missouri and their consequences for reproduction. Selected sites represent the extent of the species' geographic range and variation in population size, including populations that typically produce many stems (ramets or genets) but exhibit low seed production. Results were used to determine if low seed production was the result of a lack of genetic diversity or genotypic richness. Instead of confirming long held assumptions, her conclusions rejected the



Photo by Malissa Briggler

**Image 4.** Dr. Edwards plants Mead's milkweed grown from seed collected for genetic research. Increasing the number of flowering individuals is likely to improve seed production.

hypothesis that low seed production was due to a lack of genetic diversity within populations. Further, Edwards reported low genetic structure among populations of Mead's milkweed, indicating widespread genetic connectivity despite fragmented geographic distribution, likely because seed dispersal by wind allows individuals to move among sites (Image 3, previous page). High genetic connectivity and low structure suggests that outbreeding depression would not occur when transplanting Mead's milkweed among populations, although these results should not be taken as a recommendation to freely move and cross-pollinate Mead's milkweed across its range. Genetic integrity of populations, particularly in isolated habitats like the St Francois Mountains, remain an important concern.

One of the main conclusions of Edwards' study indicate reproduction was strongly connected

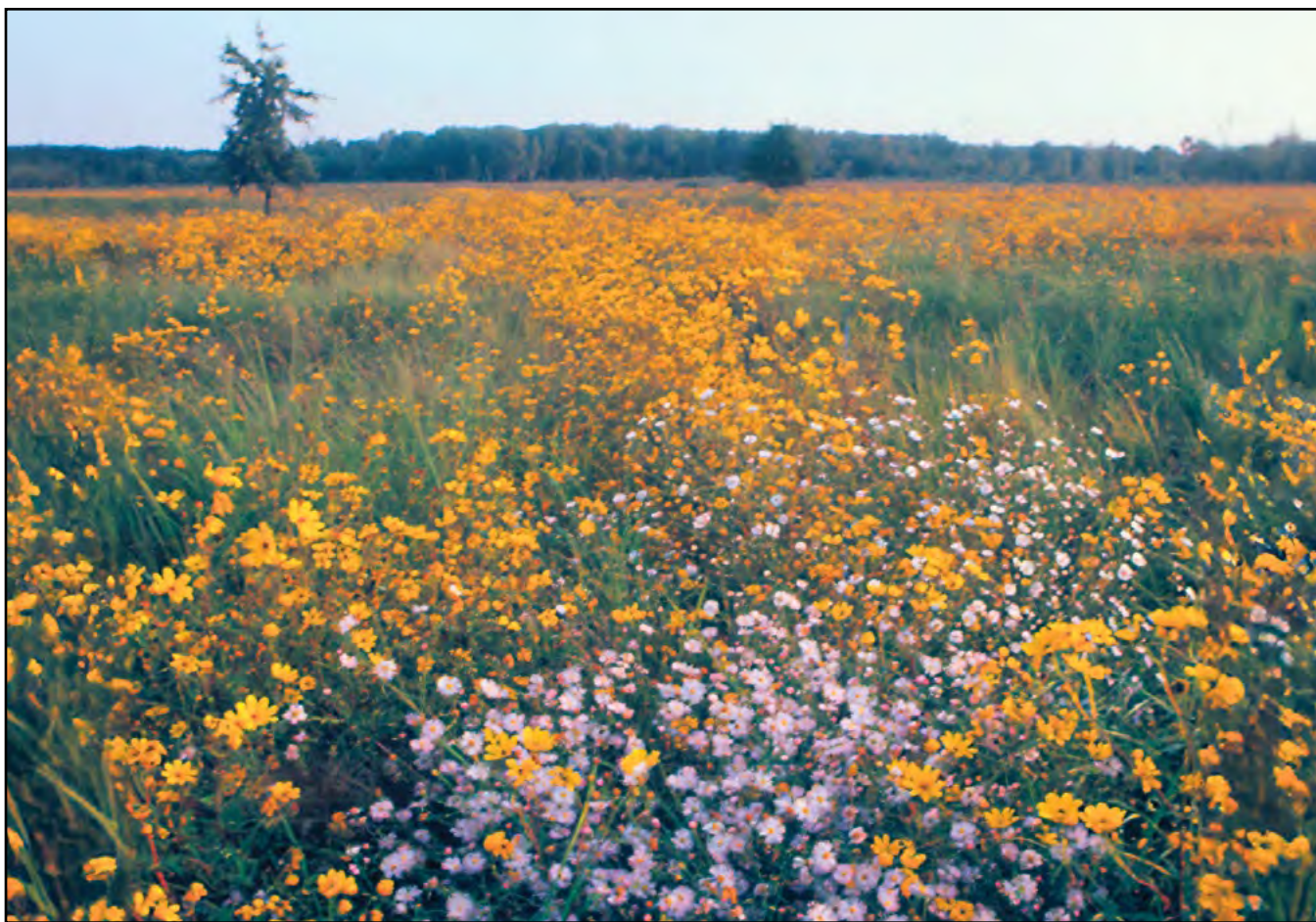
to flowering population size, with a population of at least 50 flowering stems necessary for successful seed production. To understand why this is the case, Edwards has begun a 4-year study to identify other factors that may limit seed production in small populations (image 4). Potential pollinator and pollen limitation will be examined by studying the pollinator abundance and success rates of removing pollinaria. She will investigate other potential resource limitations by conducting hand pollinations and comparing the results of small populations to those of larger populations to determine whether other resources are or are not limited in small populations. A final goal of this work will be to augment smaller populations with seed-grown transplants in efforts to overcome reproductive limitations, increase seed production, and improve the population viability. Results of this work are forthcoming in 2026.

Recovery efforts for Mead's milkweed involve a tremendous amount of cooperation and partnership. Landowners include private individuals, Missouri Prairie Foundation, Nature Conservancy, Department of Natural Resources (MDNR), Missouri Department of Conservation (MDC), U.S. Army Corps of Engineers, and U.S. Forest Service. The Missouri Botanical Garden and Powell Gardens are important partners with MDC in conducting research and transplanting efforts. The U.S. Fish and Wildlife Service Ecological Services Field Office has provided expertise and assistance in securing funding. Statewide monitoring efforts involved several volunteers and led by staff of MDNR and MDC. Many challenges and threats keep the status of Mead's milkweed a great concern. However, ongoing research and collaboration provide a hopeful future. 🌱

Malissa Briggler is the Missouri State Botanist with the Missouri Department of Conservation

Contact: [Malissa.briggler@mdc.mo.gov](mailto:Malissa.briggler@mdc.mo.gov)





**Image 1.** Historically, the wet bottomland prairie at Pershing State Park offered a colorful display of yellow, purple, and white forbs in the fall, including various species of *Bidens*, *Symphotrichum*, and *Boltonia*. This photo was published in a two page spread in *The Terrestrial Natural Communities of Missouri* (Nelson, 2010) as the representative illustration of wet bottomland prairie.

## A Prairie Persists: A Tale of Resilience and Loss in a Wet Prairie System

by Carrie Stephen

Pershing State Park sits tucked away off Highway 36 in Linn County, Missouri. It is an easily overlooked gem as you drive by, holding remnant fragments of a historically diverse system of wet prairie, bottomland forest and shrub swamp. In the floodplain of a once wild, meandering Locust Creek, several sloughs, marshes, and oxbow lakes persist. Locust Creek was a life source for these diverse communities. Today, within the park's boundary, Locust Creek is all but dry most of the year. It is only with the help

of some human engineering that the wet prairie that persists can see recharge without immense sediment loads. The story of the wet prairie at Pershing is not a particularly happy one, but it is important to share. What is shared here is just a fragment of the story. Wet bottomland prairies, ranked Critically Imperiled in Missouri, are rare among prairie types. Prairies as a whole are already grossly reduced compared to their historical extent. And so the fervent mission to save the wet prairie at Pershing SP continues (Image 1).



Pershing's wet prairie communities were not initially recognized for the splendor they possessed at the time the park was created in 1937. Pershing primarily exists from the wake of World War I when local residents wanted to honor their own Linn County original, General John J. Pershing, and his service during the war, with a national park. When the National Park Service declined the nomination, citizens recommended a state park which was pursued by the state of Missouri. At the time, the natural beauty of the park was recognized in the majestic cottonwoods in the bottomland forests and in the meandering Locust Creek, a disappearing natural feature in North Missouri as prevailing forces in the largely agricultural interface favored channelization. However, the wet prairie systems at the time of designation as a park were largely overlooked.

The wet prairie was dismissed to the degree that in the 1970's, a local park manager "put the treeless ground to good use" by row cropping it for two years. Persistent flooding from Locust Creek quickly ended the venture. Fortunately, the prairie survived and healed from this effort, and the area was soon after recognized as a good quality wet bottomland prairie by the then-nascent Natural History Program. At over 700 acres, it was the largest known wet prairie remaining in north Missouri.

By the time the wet prairie was recognized as possessing botanical value, it was likely already undergoing degradation from its historic state. The wet prairie suffered not only from a brief attempt at farming, but also from the early impacts of sedimentation and artificial retention of flood waters because of the levee system surrounding it. However, in the spring, a rich grass and sedge community dominated, particularly after a prescribed fire. The plant communities varied with minor topographic and subsequent moisture differences. Closer to

### Floods of 1993 Impacts to Pershing State Park

The summer of 1993 saw catastrophic rainfall throughout the Midwest. All time high flood stage records were broken along the Missouri River from Kansas and Nebraska to St. Louis, Missouri. On July 10, the Grand River crested at a record 42 feet at Sumner, 20 miles north of the river's confluence at the Missouri River. Flood waters from the Grand backed up 5 miles to Pershing State Park, inundating the Locust Creek floodplain. These murky floodwaters persisted for at least 30 days, covering the bottomland prairie and forest in water at least 6 feet deep. Adding to the flow event, Linn County received 14 inches of rain in July. As the waters finally receded, park ecologists observed that much of the once vibrant cover of prairie grasses, sedges, and forbs had succumbed in the month of silty, dark-standing water. Foul decay of dead vegetation followed during the summer heat. Because the Missouri River floodplain is largely covered in levee systems, this flood event was deemed unnatural. In addition, the levees surrounding the wet prairie likely contributed to unnatural retention of the floodwater. Ecologists feared that this event dramatically reduced or eliminated much of the natural distribution of prairie plant species.

the creek, a wet mesic prairie displayed compass plant (*Silphium laciniatum*), goldenrods, asters, and sunflowers. Along Locust Creek, a community of bottomland forest also housed great sedge, grass, and forb diversity.

Early on, prairie management explored methods on how to reintroduce fire to such a wet area. Ultimately, managers determined that fall and early winter burning was the most effective before snow pack and spring moisture affected fuel. Other early projects involved pushing back on woody encroachment from the treeline. In the late 1980s and early 1990s, no one involved in ecological management in the area realized the extent of future challenges.

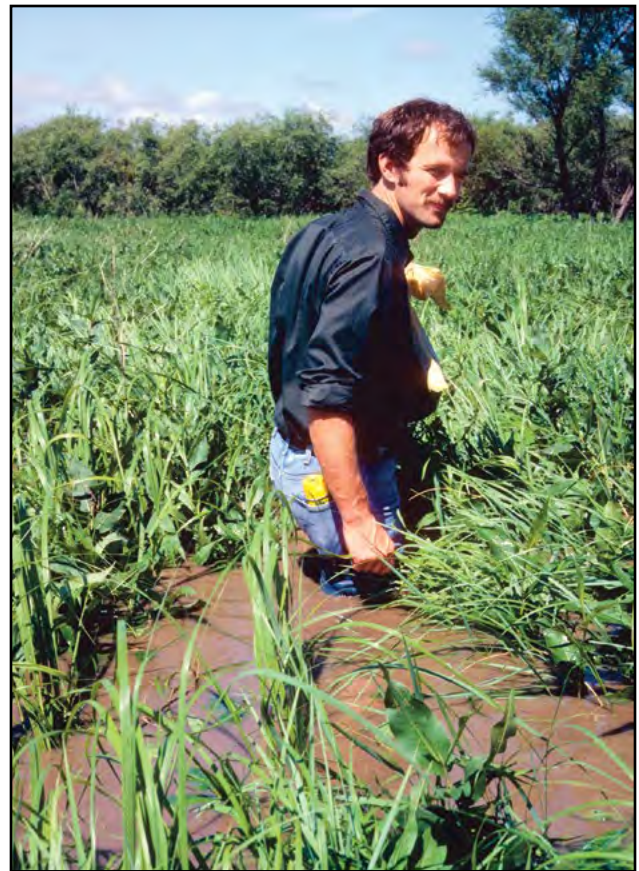
---

## The story of Cordgrass Bottoms Natural Area

---

At the time of the park's establishment, Pershing was actually home to two wet prairies. In 1979, Cordgrass Gumbo Prairie-Marsh, a 76-acre wet bottomland prairie, was nominated as the Cordgrass Bottoms Natural Area. The original nomination listed cordgrass, water smartweed, wild water pepper, and cutgrass as the dominant plant species. Other noted flora included bugleweed, common ironweed, water parsnip, blue flag iris, swamp milkweed, false aster, and a variety of sedges (such as *Carex grayii* and *Carex hyalinolepis*). Unfortunately, this prairie did not persist throughout the years—instead, through time, it was buried by several feet of sediment due to unnatural flood events from Locust Creek. Among the few photos that remain of historic Cordgrass Bottoms is of then-Chair of the Missouri Natural Areas Committee and Director of the Natural History Program from Missouri State Parks, Paul Nelson, standing knee high in cordgrass and sedges during a flood pulse on Locust Creek (Image 2). During 30+ years of sedimentation, cordgrass disappeared from the natural area as it morphed into a doghair thicket of silver maple and reed canary grass. The Committee delisted Cordgrass Bottoms NA in 2014 as the defining feature of wet prairie no longer existed.

Historically, Locust Creek was the lifeblood of the wetlands at Pershing State Park. Due to upstream channelization, land clearing, and row cropping into the riparian corridor, Locust Creek began carrying an excess of logs and sediment, which had become the largest threat to these complex wetland systems. By the late 1980s, ecologists with Missouri State Parks began to note issues that come part and parcel with excess sedimentation. In the 1990s, the Missouri Department of Natural Resources began a strategy of acquiring land to create buffers to filter and trap sediment in the streambed, with the intention of preventing intense sedimentation



Missouri Department of Natural Resources file photo

**Image 2.** This 1979 photo shows former Natural Areas Coordinator, Paul Nelson, with a collecting bag of sedges in Cordgrass Bottoms NA during a flood event. This natural area was delisted in 2014 as the wet prairie no longer exists and today the area is a thicket of silver maple and smartweeds, supported by excessive sediment.

further downstream where remnant wetland communities still thrived. Although this strategy was well-founded, land acquisition was a slow process. By the late 1990s, sedimentation grew to a severe problem.

---

## Sedimentation and log jams at Locust Creek

---

The threat of sediment loading is three-fold. In the forefront is the sheer amount of sediment traveling downstream to the park. Heavy erosion upstream results in significant sediment loads that bury native vegetation. This amount of sedimentation also homogenizes topographic diversity, which affects moisture gradients and resulting plant communities. Second, the high levels of sedimentation build ground quickly,





Missouri Department of Natural Resources file photo

**Image 3.** Bottomland forest filled in with sediment after a major flood event. Vegetation has been completely buried. Prior to flooding, these forests hosted diverse flora including spring wildflower displays and Pale Green Orchid where the forest edge met the wet bottomland prairie. The pale green orchid population was lost due to 2 feet of sediment deposition.

such that creek dynamics change more drastically than before. One major change is that the creek bed continues to rise due to sedimentation, which then creates pressure upstream and a greater possibility of flow diversion away from the original creekbed. A 2013 U.S. Army Corps of Engineers (USACE) study on the Locust Creek Watershed estimated that Locust Creek had risen between 2 and 4.5 feet between 1974 and 2013. In 2017, monitoring determined that the Locust Creek channel sits higher than most of the floodplain around it. Because of the amount of sedimentation, the channel continues to rise more quickly than in the past. Third, sediment loads bring in nutrient flushes which cater to a different community of vegetation—weedier species such as invasive reed canary grass.



Missouri Department of Natural Resources file photo

**Image 4.** Wet bottomland forest at Pershing State Park hosted moderate vegetative diversity prior to excessive sedimentation. Flora included ostrich fern and various sedges with an overstory of large cottonwoods, oaks, and silver maples. Indiana bats have also been found in this forest. The trees remain, but much of the flora has been lost.

Sedimentation has affected all of the wetland systems at Pershing State Park, including the former Cordgrass Bottoms NA, the 700-acre wet-mesic and wet bottomland prairie further south in the park, the bottomland forests, and the shrub swamps (Image 3). The park lost its only known population of the state species of conservation concern pale green orchid (*Platanthera flava* var. *flava*) in the 1990s after a large sedimentation event (Image 4). The location of that population sustained a 2 foot load of sediment, and the orchids have not been seen since. The sheer quantity of sediment over time is difficult to overstate. For example, at Locust Creek Covered Bridge State Historic Site, the current foundations for the bridge are 14 feet higher than the original foundations. The



foundations of the bridge were raised multiple times because of the sedimentation. Today, the covered bridge rests squarely on solid ground of what was once the creek. Plans are underway to relocate the historic site to a more sustainable location. Sedimentation also buried a remnant wet prairie, known as the Massie tract, owned by The Nature Conservancy and leased to Missouri State Parks to add to the larger wetland matrix at Pershing. Both before and during mitigation efforts, an entire wetland mosaic has lost a great amount of its diversity due to years of repeated sedimentation events.

Because Locust Creek meanders through Pershing, though is channelized north of the park, Pershing also finds itself the location of numerous log jams. Small log jams were part of the park's history for a long time and had not caused significant issues downstream in the park. When the first major log jams appeared at the park in 1993 shortly after the historic Mis-

souri River floods, management viewed these as a natural part of the creek system. In a previous landscape with a gentler anthropogenic influence, these log jams were normalized as a natural function of the system. Over several years in the 1990s, park management grappled with public opinion on removing the logs, as large logjams affect flooding and farmland in the larger watershed. During that investigation period, the creek adjusted in sections of the log jam on its own—it meandered around or sometimes through the logjams, and deposited sediment on top of the logs which quickly filled in with vegetation, and formed a new channel.

By 1995, with more flooding impacts, more logjams accrued further north in Locust Creek. Although the creek adjusted to the logjams and sediment loading in some sections, other areas became more severely plugged and did not have any clear path for the water to run around or through (Image 5). During a high flow event in

**Image 5.** A logjam has filled Locust Creek from bank to bank in 2021. This log jam began accruing in 2019 and by 2021 extended for 1.25 miles. Work on this particular log jam began in 2021 and continues today.



Photo provided by Dustin Webb, Missouri Department of Natural Resources

the creek, log jams rerouted overflow directly through the bottomland forests and into the wet prairie. The high flow event filled the sloughs and other wet depressions with sediment, and with the sediment came reed canary grass and other undesirable vegetation. Sections of bottomland forest and wet prairie were buried. This was a historic turning point for how the park would address future log jams and the threat of immense sediment loads. With the amount of erosion occurring upstream due to changing land use practices, the park no longer felt that the creek and surrounding wetland systems could accommodate the number of log jams, the speed at which they grew, and the immense sediment loads without great risk of losing the wetland systems all together. Thus in 1996, the park staff began managing logjams.

Early on, logjam management was primarily conducted with bank-packing. The park modeled the technique after observations of what the creek does on its own, but aimed to speed the process up to prevent a repeat of high flood events depositing large sediment loads in the bottomland forests and wet prairie. That is, park staff packed logs into the inside of creek bends to create point bars and thus formed a pilot stream on the outside which the creek itself then widened. By utilizing the inside of creek bends, the creek would naturally deposit sediment on the log debris, which encouraged vegetative growth. Sediment and vegetation together helped lock point bars in place. This method met some resistance early on, particularly with concerns over whether the logs would remain locked in place in the constructed point bars. Ultimately, the point bars were successful and continued like natural point bars, and thus re-vegetated relatively quickly.

Throughout the 1990s and into the early to mid-2000s, bank-packing was the method the park used to address log jams. But the log jams kept coming, new channels kept forming, and more sediment was depositing. Managing log-

jams became a major challenge. Additionally, sedimentation was causing the creek channel to rise. These two facets of ecological issues applied pressure to upstream flows, slowing down the upstream flow. Consequently, Locust Creek naturally did what any creek would do when faced with a massive plug—reroute to an easier path. This reroute took Locust Creek and much of its flow to Higgins Ditch.

Higgins Ditch is a straight channel, created by farmers in the area to drain their crop fields during flood events long before massive logjams started to plague Pershing. It lies less than three quarters of a mile west of Locust Creek where they both pass under Highway 36. The wet prairie lies in between Locust Creek and Higgins Ditch south of the highway. Amidst the monitoring, debating and scrambling to remove the many log jam problems along Locust Creek, water found an easier route and began to head cut towards Higgins Ditch just north of Highway 36. Park managers noted their concerns early on, when the headcut was quite small, but the evolution of the headcut to a complete reroute of the creek was swift—at least faster than the park could respond. With subsequent high flow events and logjams, Locust Creek completed its path to Higgins Ditch. At that point, large amounts of flow were pirated away from the original Locust Creek on a regular basis. With that pirating, flood events (with excess sediment) were also a threat from Higgins Ditch.

To be clear, the headcuts likely began with early sedimentation and before the first major logjams. But subsequent and rapid accumulations of logjams greatly sped up the process. Efforts were made early on to prevent water pirating to Higgins Ditch. Park managers installed gradient control structures in 2007 to restore flow to the original creek. Although these structures were relatively effective early on, the pressure they had to withstand was trying, and park managers realized quickly they would need to continue taking action. In 2009, park



staff notched some levees to relieve pressure on the gradient control structures. In 2012, with the help of some grant dollars, MDNR added several more gradient control structures. However, at a certain point, yet another log jam formed at these structures and that, combined with record flooding, compromised their functionality. A tipping point was reached, and the cut-across channels quickly became the new primary path of Locust Creek. The bulk of that water flowed directly into Higgins Ditch, leaving the original channel of Locust Creek all but dry. In 2010, it was determined that Locust Creek channel sat over 10 feet higher than the Higgins Ditch channel. With this difference in elevation, maintaining flow in Locust Creek has proven to be a losing battle.

Consequences of the loss of flow in this section of Locust Creek affect species beyond the terrestrial wetland communities around the creek. The flat floater mollusk (*Utterbackiana suborbiculata*) and trout perch (*Percopsis omiscomaycus*) were both species that have lived in Locust Creek within the park boundary. The flat floater is considered imperiled and the trout-perch is critically imperiled in Missouri. Since the creek has been pirated away, neither species have not been found within the park boundary. Locust Creek maintains a greater flow south of the park where tributary streams and creeks restore flow, and so these species may persist in other areas, but their habitat has certainly been diminished.

---

### The story of Locust Creek Restoration Area and Locust Creek Wet Prairie

---

Although Cordgrass Bottoms was lost to sedimentation, Pershing has seen some successes in wetland management. To protect the larger wet prairie further south, MDNR partnered with the Natural Resources Conservation Service (NRCS) to create a buffer zone with land acquisition—an area that could filter out the large sediment loads while still allowing water to recharge the wet prairie. The goal was to restore this former soybean field to wetland to function

as an extension of the current wetland systems and provide additional habitat for wet prairie and marsh communities. With some additional federal funding, in 2009 MDNR purchased 1,449 acres divided into two units as a part of the Locust Creek Restoration Area project.

This land was historically used for agricultural production for years, and was located where it could absorb some of the sediment pulses that were coming from Higgins Ditch and Locust Creek. Together, NRCS and Missouri State Parks developed a wetland restoration plan, which involved engineering a flat agricultural landscape into a riparian floodplain. In the mid-2000s, MDNR and NRCS implemented the plan to construct berms and other structures to mimic oxbows, ridges, and swales so that floodwater could be guided through the system and thus mimic the historic wetland landscape. During flood events, this LCRA wetland allows for sediment deposition in the restoration area instead of in the wet prairie itself. Over time, with the cooperation of other land owners, some of the levees were dropped to allow water to sheet over them in a manner that would better replicate water flow in a floodplain. This sheeting also helped move sediment through the system without too much deposition in any one location.

Additionally, massive amounts of seeding and planting of cordgrass plugs have contributed to a vegetative restoration of the area. The restoration is maintained with fire to prevent woody encroachment. Because the area is essentially a sedimentation catchbasin during flood events, some areas favor a lot of weedy (and even invasive) species like reed canary grass, but as a whole, the restoration has offered an excellent opportunity for wetland habitat expansion. In fact, prairie massasauga rattlesnakes (*Sistrurus tergeminus tergeminus*), which have lived in the wet prairie for many years, have colonized the LCRA. Prairie massasaugas are state endangered, so the expansion of their habitat at the park has been an exciting affirmation of the success of the Locust Creek Restoration Area.



Overall, this restoration area offers protection for what remains of the wet prairie. The LCRA successfully filters sediment from high flow events in Higgins Ditch. As effective as LCRA is, the truth remains that the wet prairie is not the same as it was 30 years ago. Years of sedimentation have resulted in what seems like seas of reed canary grass encroachment and the reduction of many of the native grasses, sedges, and forbs that covered this area years ago, not to discount the impact of a teeming deer herd, managed annually with Managed Deer Hunts. Reductions in the herbaceous diversity from sedimentation and deer herbivory have impacted invertebrate and bird populations (Image 6). Still, pockets of that original wet bottomland prairie containing prairie cordgrass, bulrush, asters, and other various sedges continue to persist though in diminished populations.

Restoration efforts are not complete, and challenges remain. The wet prairie has lost its lifeblood from Locust Creek due to lack of flow. Although Higgins Ditch has, in the recent past, offered hydration as routed through LCRA, the ditch has deposited so much sediment in LCRA that flood waters no longer filter through the way they did upon original design of the wetland project. Instead, floodwaters remain channelized in Higgins Ditch or overbank in the western reaches of the park. Logjam projects continue—to date, MDNR has removed or treated at least 30,463 feet of logjams. The Department has spent over \$1.9 million on logjam projects, which does not include contributions from other agencies. These numbers continue to grow every year. Logs are now often removed, and not just packed into banks due to the quantity. Although the cost of removal varies, on average, it costs \$100/linear foot of logjam, which adds up quickly considering the park has addressed miles of logjams over the years.

The invasive common reed (*Phragmites australis* var. *australis*) has posed a new threat. While this species has not colonized the wet prairie, it grows



Photo by Carrie Stephen, Missouri Department of Natural Resources

**Image 6.** The impact of deer overbrowse on native forbs at Pershing leading to additional instability of the natural communities cannot be underestimated.

in the LCRA. Common reed is a challenging species to remove, although preliminary drone treatments have proven promising.

As overwhelming as the challenges can be, the wet prairie persists, and we are still trying to save it. Even without hydration from the creek, the soils still hold water well from precipitation, and those moisture-loving species have managed to continue to make their home there. Buttonbush still sticks out in the swales. Bulrushes stand tall. The cordgrass, sedges, iris, white beardtongue, false asters, saw toothed sunflowers, and obedient plants still persist in beautiful little pockets if one takes the time to find them. 🌿

---

Carrie Stephen is a Natural Resource Ecologist for the Missouri Department of Natural Resources.

Contact: [Carolyn.stephen@dnr.mo.gov](mailto:Carolyn.stephen@dnr.mo.gov)



**Image 1.** Prairies in the Midwest may see dramatic climatic changes that will make the growing conditions less suitable for prairie plants. Ecosystems cannot migrate to escape climate change, and planting facsimiles of our existing natural communities will never recreate the complex soil properties of communities as they exist today

# Where Will Midwest Ecosystems Be In 2500?

by Adam B. Smith

Recently, I experienced the dubious pleasure of reading a horror paper. Like a horror novel or horror movie, a horror paper is one that propels you to keep on a nightlight when you go to bed, or to hesitate to look behind the shower curtain. The paper's title was "Climate change research and action must look beyond 2100," written by Christopher Lyon and colleagues (Lyon et al. 2022). The gist of the paper is that when we discuss future climate change, we often stop at the year 2100, or even before, for the simple reason that 2100 is a nice, round number.

In a sense, humanity has pushed a well-balanced boulder off a ledge—once rolling, it requires a lot of effort and time to stop the momentum.

The best-case warming scenario in reviewing climate science requires an immediate break in carbon emissions and a technologically challenging "drawdown" of carbon from the atmosphere. Only under this scenario does the "climate boulder" come to a slow roll within this century.

All climate change scenarios continue apace. The next-best warming scenario is dubbed "RCP 4.5," which stands for "Representative Concentration Pathway where anthropogenic heating reaches an extra 4.5 Watts/m<sup>2</sup> above background levels by 2100." Given where we are in 2023, RCP 4.5 may be barely achievable politically, economically, and technologically. The worst-case scenario, RCP 8.5, places us at



global mean temperatures between 5 and 9°F higher than the pre-industrial baseline by 2100. Luckily, we are not on this worst-case pathway as it requires more fossil fuel emissions above our current use. However, examining that most feasible best-case scenario, RCP 4.5, eventually we reach temperatures that are expected in the range of the worst-case scenario, though this only happens past the year 2300 (Lyon et al. 2022). In other words, we eventually reach the worst-case scenario, it's just a matter of time.

The authors of the horror paper describe changes expected across the Midwestern US in the next several hundred years. It is comparatively easy to imagine the region becoming moderately warmer—ecosystems will be strained and may shift somewhat with climatic changes, though ecosystems cannot transport all of their facets, but we cannot expect habitats far afield to be favored here. Fast forward to the 26th century, when (depending on emissions), we might be living under a sun that feels 14° hotter and when the Midwest climatically resembles a subtropical or tropical system. Under this future, the authors of the horror paper appeal to science fiction and even include fictional imagery of a future Midwest populated by palm-like trees fit for the new norms of the far future. The authors' argument is not that they necessarily expect a tropical system to develop, but rather that this shift will be so dramatic that conceptualizing it requires imagination beyond simply looking at the “next ecosystem over” to see what's coming. But even in 2023, mid-Missouri gardeners are able to grow and maintain Southeastern US garden species such as banana (*Musa* sp.) and ornamental canna lilies just with a thick layer of mulch protection through the winter.

This is what keeps me up at night—how do we anticipate and work for a future that will rewrite what the Midwest is, and will be in the future?

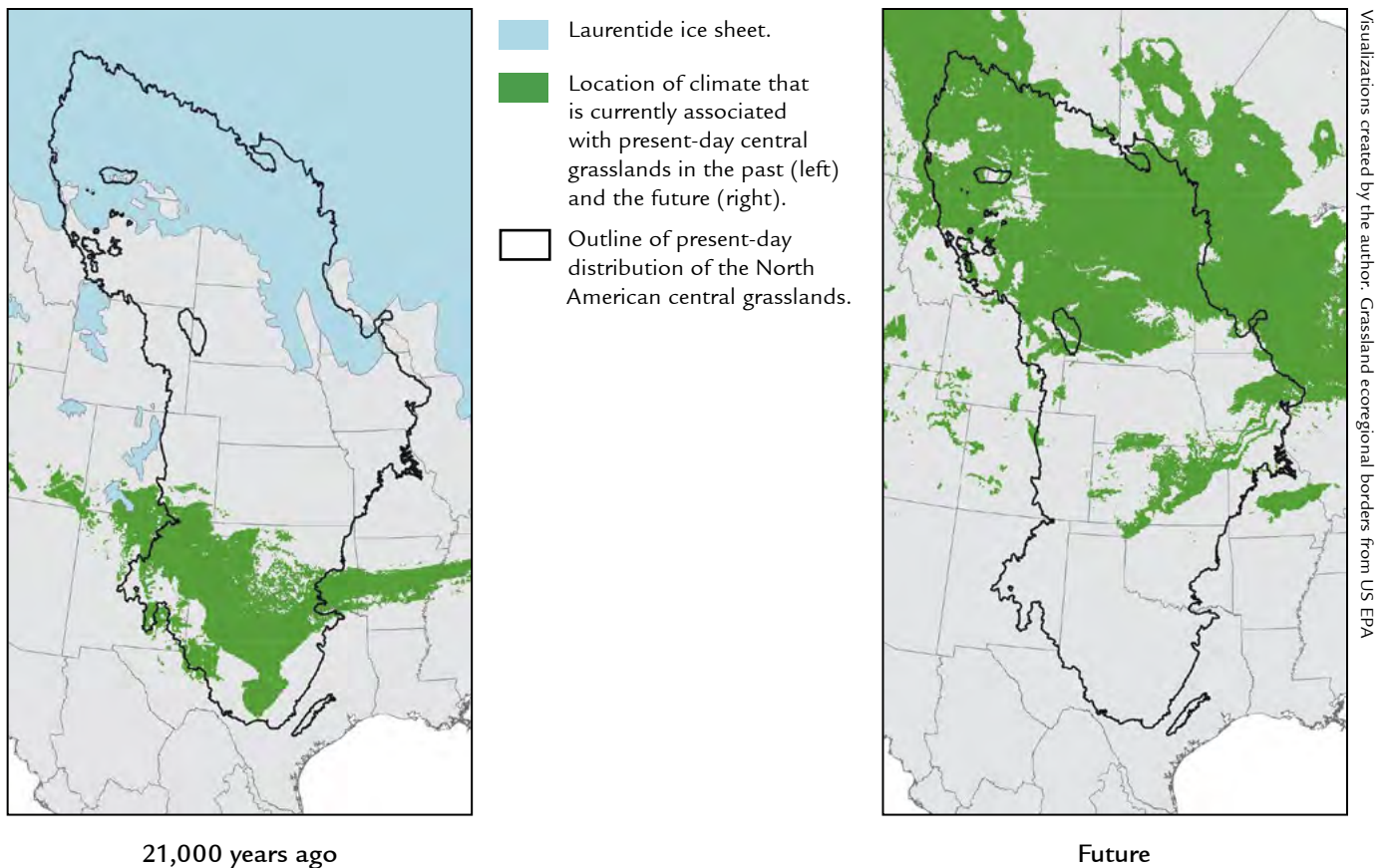
First, a basic question: Why should we, today, care about what may happen several hundred years from now? One good argument for keeping it in the back *vs.* the forefront of the mind is that we need to manage this century for the future populations to have ecosystems to live in and to work within. This means we need to manage our prairies, woodlands, forests, riparian corridors, wetlands and all other natural communities in order that we can bequeath these precious gems to the next generations. This is sound reasoning, manageable, and if it belays irrational fears about what may be lurking behind the shower curtain, then this reasoning is well worth the thoughts.

However, ignoring what seems the “far” future is repeating the iniquity of “passing on the problem” to future generations that begat the same crisis we face today. We were first warned about the potential for anthropogenic climate change 180 years ago when Eunice Newton Foote astutely observed the heat-trapping capacity of carbon dioxide in the atmosphere. This and other warnings were not inaccessibly buried in academic texts; by the 1950s, popular television science shows alerted viewers to the possibility of anthropogenic warming (Bell Science Hour, 1958<sup>1</sup>). For myself, I expected to see the striking weather patterns of the past few years—visible wildfire smoke spreading across half the country, unprecedented drought, and whiplash polar vortices momentarily mimicking winter conditions of the 1970s, then springing back to the “new normal” of mild wintertime—by 2050. For me, “climate change” was science fiction, something that would happen in the future which I'll only experience if I'm lucky to live that long. Ignoring the problem of the current future compounds our debt to the impending future, even if that future is several hundred years yet in the making.

The reality is that the impending climatic changes will rewrite the biological text of the

---

1 [https://www.youtube.com/watch?v=xIph\\_7CJq4](https://www.youtube.com/watch?v=xIph_7CJq4)



**Figure 1.** The past and future location of climate that is currently found within the North American central grasslands. When glaciers reached their maximum extent 21,000 years ago, climate indicative of present-day grasslands was far south of most of where it is today. In the future, climate of the region will move northward, leaving the fate of the central grasslands an open question. The location of a particular climate does not necessarily imply occurrence of specific ecosystems that are currently associated with that climate. The future scenario here is based on projections to 2070 under the worst-case warming scenario using the most extreme climate model. Even if this scenario does not come to pass by 2070, something like it will in centuries to come.

Earth, and that text is comprised of the ecosystems we manage and depend upon. Much of the philosophy of present day management activity assumes that the past is the best guide to the future (and even the “standard” for what one should manage. Lynch et al. 2021). But impending changes will not allow for the maintenance of the status quo as a possibility. To illustrate, in Figure 1, the Midwest ecosystems could conceivably exist, climatically speaking, under the “worst-case” scenario farther north (RCP 8.5) by 2100. This, of course, is taking into account that under less-worse scenarios we will eventually reach the same amount of change, albeit later. Figure 1 also illustrates the Midwest’s climate 21,000 years ago during the

Last Glacial Maximum, which is the time when the northern ice sheets reached their greatest extent across North America.

One may be able to witness that future changes are as dramatic as the climatic changes from the past. However, these future changes will play out over the next few hundred years, in contrast to past changes which occurred over many thousands of years. Consider a mythical position, say, if one was a land manager during the end-Pleistocene, just as temperatures began warming and the glaciers began the great retreat. What would have been a land manager’s management options? Manage for the “present” and push back against these global-scale forces affecting the land, or somehow adapt?



Under the Resist-Accept-Direct (RAD) framework, management actions can be classified into whether they retain the present-day state of a system despite outside pressures (resist), allow changes as they come (accept), or actively manage the system as it changes so it is likely to enter a desirable state (direct) (Lynch 2021; National Park Service, 2021; Schuurman et al. 2022). The appeal of this framework is that it encompasses all possible management strategies (including doing nothing—which typically aligns with “accept” (Schuurman et al. 2022).

Another appeal to RAD is that actions are not necessarily exclusive. We might accept a certain change (e.g., replacement of a dominant, climate-sensitive species for another), resist other changes (e.g., prescribed burning at historical

rates), and direct elsewhere (e.g., introducing large, non-indigenous grazer species that help maintain historic channels and levels of energy flow through the system). Likewise, adopting one of the prongs of the RAD framework does not preclude adopting another later in time.

As an example, consider how the grass Big Bluestem (*Andropogon gerardii*), a “workhorse” species of the tallgrass prairie, could shift in its dominance and distribution. Currently, this species is so iconic of the tallgrass ecosystem that prairie restorations are almost obliged to include it because it simply would not be a prairie (or function like one) without Big Bluestem. Its “core” range comprises the multi-state region of northern Missouri, Iowa, Illinois, and Indiana, and a bit of the neighboring states (Figure 2).

**Figure 2.** The present-day and potential future “core” of the range of Big Bluestem. The ecotype in the core is the tallest variety, but in the future, a knee-high ecotype, currently in western Kansas and eastern Colorado, may be favored in the present-day core. Meanwhile, conditions conducive to the tall ecotype will move northeastward. Even if this potential future does not come to pass this century, something like it will occur in subsequent centuries. Visualizations created by the author and based on Smith et al. (2017).

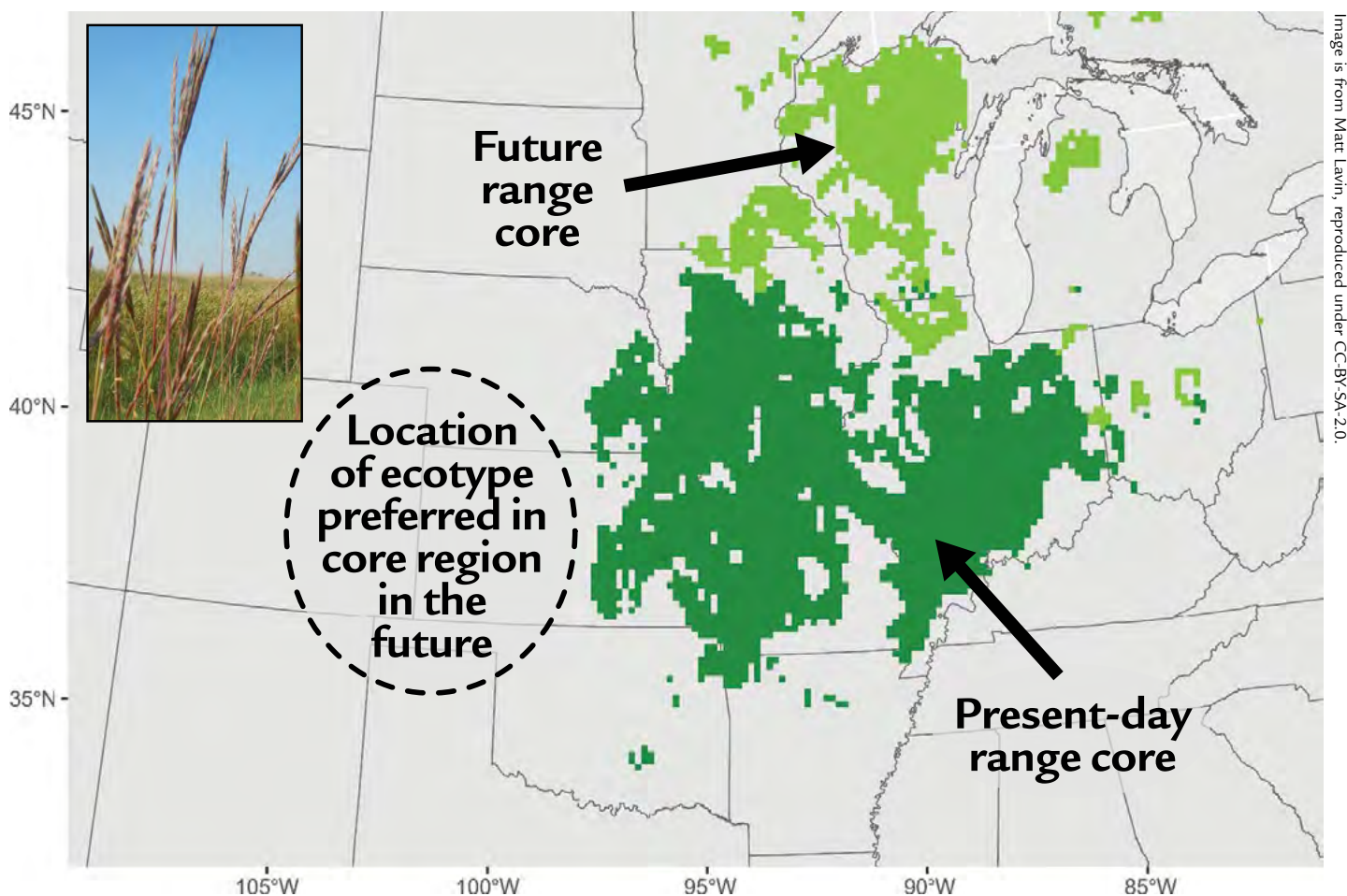
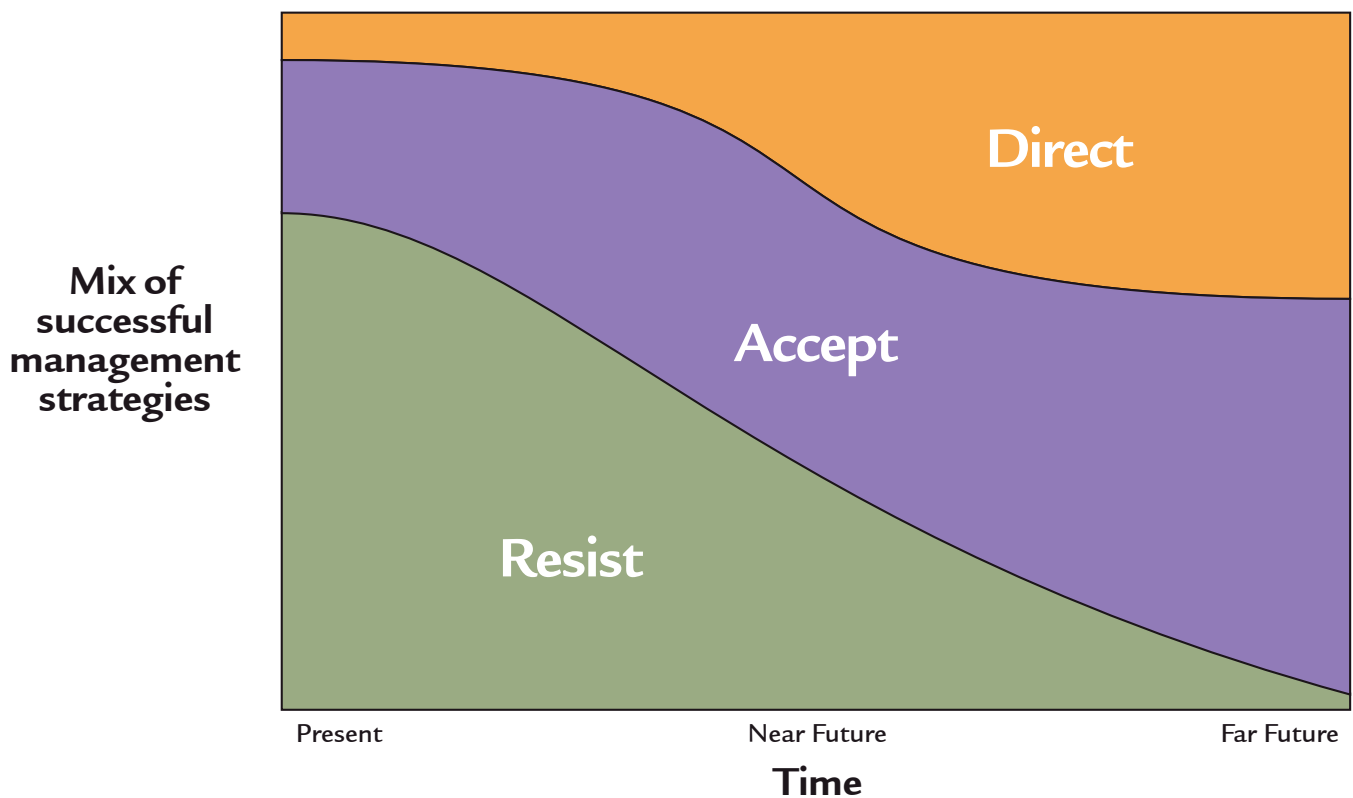


Image is from Matt Lavin, reproduced under CC-BY-SA-2.0.



**Figure 3.** As time passes and climate change continues apace, the percent of “resist” strategies that are successful will decline. In its stead, “accept” and “direct” strategies may be more successful.

However, my colleagues and I project that by the late 21st or early next century, the climate indicative of this core area—and Big Bluestem’s dominance—will have shifted to the Great Lakes region and into lower Canada. In its place will be climatic conditions currently favored by the short ecotypic version of the species that now inhabits western Kansas and eastern Colorado—500 miles westward of where it will need to be for the same functionality (Smith et al. 2017).

Under the RAD framework, current restorations aptly apply the “resist” framework, managing for grasslands that are generally intended to mimic what they had been pre-European settlement. At some point, though, *resisting* change will become harder. Continuing the example, at some point, climatic conditions in the core of Big Bluestem’s range may become unfavorable to the tall form, causing it to give way to more drought-tolerant varieties or species. Managing prairies as if they could still support the tall

variety will become an increasingly arduous task of *resistance*. We may choose to accept what comes—which may or may not include wholesale decline of Big Bluestem. Alternatively, we could draw seed from far-afield climatic conditions to assist species’ accommodation to changing environmental conditions in order to *direct* the system to a state where Big Bluestem still plays a role, albeit likely a diminished one.

As large as these changes seem, they are small steps compared to what comes in the subsequent centuries. As these changes come, resistance will become increasingly costly and infeasible (Figure 3). To be sure, every option in the RAD framework has costs, even “accept.” At some point, managing for the past will become prohibitive. Moreover, if we hang on to a “resist” management stage too long, then it may make more costly subsequent shifts to “accept” or “direct” stage. Continuing our example even further, sourcing seed for restoration from nearby



locales is desirable because species tend to be locally adapted. But given that Big Bluestem can live up to several decades, investments in locally-sourced seed will create a prairie that could become climatically “behind the times” in the sense that the ecotypes established there are no longer fit, but still dominant enough to suppress seedlings of ecotypes from farther away that would be climatically capable.

Everything I have read on the RAD framework opines that we do not have good guidance on when to resist, adapt, or direct, and when to switch between them. In any case, it is impossible to give useful advice since each situation is so different. But, very surely, “resist” will eventually fail us, if not in this century, then in the coming ones. These coming changes are fictional in the sense that they have not yet happened, but all of the future is a fiction until it becomes the present. How can we keep the “long future” in mind as we manage for the near one? 🌱

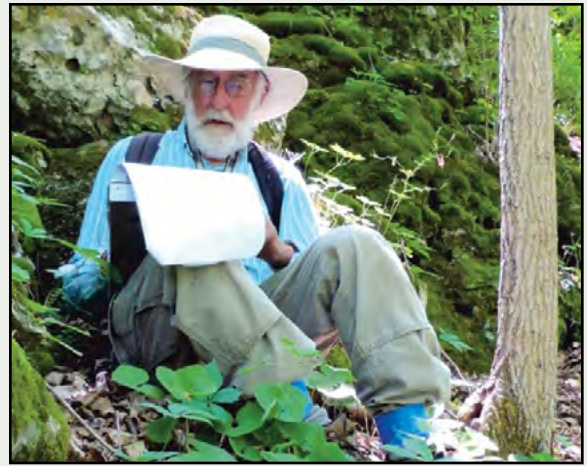
Adam B. Smith is an Associate Scientist in Global Change at the Center for Conservation and Sustainable Development within the Missouri Botanical Garden

Contact: [adam.smith@mobot.org](mailto:adam.smith@mobot.org)

#### Citations

- Lynch, A.J., Thompson, L.M., Beever, E.A., Cole, D.N., Engman, A.C., Hoffman, C.H., Jackson, S.T., Krabbenhoft, T.J., Lawrence, D.J., Limpinsel, D., Magill, R.T., Melvin, T.A., Morton, J.M., Newman, R.A., Peterson, J.O., Porath, M.T., Rahel, F.J., Schuurman, G.W., Sethi, S.A., Wilkening, J.L. 2021. “Managing for RADical ecosystem change: Applying the Resist-Accept-Direct (RAD) framework.” *Frontiers in Ecology and Evolution* 19:461–469.
- Lyon, C., Saupe, E.E., Smith, C.J., Hill, D.J., Beckerman, A.P., Stringer, L.C., Marchant, R., McKay, J., Burke, A., O’Higgins, P., Dunhill, A.M., Allen, B.J., Reil-Salvatore, J., and Aze, T. 2022. “Climate change research and action must look beyond 2100.” *Global Change Biology* 28:349–361.
- National Park Service. 2021. “Planning for a Changing Climate: Climate-Smart Planning and Management in the National Park Service.” USNPS.
- Schuurman, G.W., Cold, D.N., Cravens, A.E., Covington, S., Crausbay, S.D., Hoffman, C.H., Lawrence, D.J., Magness, D.R., Morton, J.M., Nelson, E.A., and O’Malley, R. 2022. “Navigating ecological transformation: Resist-accept-direct as a path to a new resources management paradigm.” *BioScience* 72:16–29.
- Smith, A.B., Alsdurf, J., Knapp, M. and Johnson, L.C. 2017. “Phenotypic distribution models corroborate species distribution models: A shift in the role and prevalence of a dominant prairie grass in response to climate change.” *Global Change Biology* 23:4365–4375.

Photo by Kathy Bildner



## In Memoriam: Nels Holmberg

*[Nels performed bryophyte and flowering plant surveys for many Natural Area nominations (Labarque Creek, Hickory Canyons expansion, Huzzah Narrows, Mingo,) and was a great person and teacher.]*

Nels Holmberg, well-known to the botanical and greater conservation community in Missouri, passed away peacefully at his Franklin County home on February 9th, 2024. Born in Oklahoma in 1941, Nels attended Oklahoma State University and earned a MS in biochemistry in 1966. In the same year, he married Sandra Wingate of Wewoka, Oklahoma. They spent three years working in Oxford, England, and then both came to Washington University in St. Louis for careers in research.

In 1998, Nels retired from Washington University to become a field botanist. He received his second Master’s degree in Conservation Ecology from UMSL on his 60th birthday. Nels went on to become an expert in plant and bryophyte identification, collecting more than 5,000 specimens of plant species for the Missouri Botanical Garden including 10 state bryophyte records. For 18 years, Nels led botany trips and hikes for nature study societies, reflecting his enduring passion for introducing people to the natural world, especially small organisms like insects, mosses and lichen that often go unnoticed. He also played a role in encouraging Don Robinson to donate his land for what now is Don Robinson State Park/LaBarque Creek Natural Area.

He was awarded the Missouri Native Plant Society Arthur Christ Research Award in 2006 and the Webster Groves Nature Study Society Lifetime Achievement Award in 2013.

Nels is survived by his wife Sandra and children Anne Jespersen, Jon Holmberg and grandchildren David and Sarah Jespersen; and Samantha and Kate Holmberg.





**Image 1.** Flourishing unburned high-quality woodland in Boone County.

## The Persistent Threats of Dominance & Hierarchy

by Justin Thomas

*Disclaimer: The following pointed and philosophical article is intended to stimulate thoughtful discussion. All of the opinions and thoughts expressed in the article are the author's own and not in any way endorsed or vetted by the Missouri Natural Areas Committee or the Missouri Department of Conservation.*

**T**he greatest threat to the viability and resilience of natural areas is our inability to make the majority of our mind-sets accepting of landscapes in states of natural quality. Ecological systems naturally cascade to approximations of stability over time, yet human ecological interaction and management are not at all about stability. This is especially

true with disturbance ecology twisted into conflicting definitions. Even well-intentioned conservationists are unwittingly hung up on a perverted and destructive rendition of the “intermediate disturbance hypothesis” that continues to damage natural areas. Few are open to concepts like functional dynamism. Case in point, I am willing to wager that no one will attempt to fully understand the following complex sentence: The degree to which we change our view of the world is literally the degree to which we increase the functional stability of living systems in increasing proportions toward dynamic equilibria. This sentence is



less complex than the simple complexity inherent to nature, yet most abandon the exercise with closed minds and impending cognitive dissonance. In a world that increasingly lacks complex functionally dynamic stability and a people that only want simple ideas, natural areas are not only cursed to forever be remnants but they are destined to become forgotten fables of the past.

Considering the role of humans in modern landscapes, the rarity of natural areas, and the unlikelihood of immature areas maturing into natural areas even when managed by well-intending conservationists, the only hope is abandoning our religious and colonialist mentalities for holistic coexistence through compassion. In short, we need to spotlight the psychology of ecology. Compassion offers a portal. The word compassion literally means “to suffer with.” It doesn’t mean “to feel sorry for” or “force compromise upon,” it means “to sacrifice for” and “to share the pain.” These are very different things than what we do. Even the most conservation-minded of us are light years from that even in our most well-intended forms of management and engagement with living systems.

The most endearing, most defining, most admirable quality of the living systems we are embedded within—the air we breathe, the food we eat, the beauty that inspires us—is that they establish and persist completely on their own when they are not perturbed or exploited. An American Bison is not just a bison, it is an emergent property of grassland. A Showy Ladyslipper is not an orchid nearly as much as it is the manifestation of wild engagements and myriad processes that are stable and predictable enough over vast periods of time to produce and sustain such intricate and ordered complexity. They are metabolic potentialities come to life. They are

the expressions of system states. Just as genes have no function in a test tube, perceiving an organism as anything other than a mere pixel of a larger image is foolish. They are both pixel and image, simultaneously.

Living systems have all the potential they need to regenerate and to stabilize into the complex, highly functional systems we call natural areas. Two exponents dictate the fruition of this process. The first is time. How much time is relative to how simplified a system has become and how much potential it has for recovery? The second is our ability to stay out of the way when staying out of the way is needed. Staying out of the way can include being compassionate about conditions and assisting with forward progress, but it cannot include compromised, ignorant, or passionless approaches. It means engagement and awareness not “management.” It means engaging sites and systems less like farms and more like a phenomenon. It means figuring out how they can manage themselves. Management has proven to be ineffective to this larger goal, if not damaging of the larger goal, to degrees that management should be avoided at all costs in lieu of compassionate engagement with natural tempos and potentials—which is how management is often intended, but seldom intentionally delivered.

Because modern humans are burdened with the traumas and dysfunctional ideologies of our religious and colonial past, we have tremendous trouble overcoming our destructive engagement with living systems even when we mean well. Our attempts to make things better result in programs that stock declining species and systems (Hellbenders, Spoonbills, prairie restorations, etc.) in habitats that are too degraded to support them, rather than improve the habitats to healthful conditions; enforce totalitarian regulations on the harvest-





**Image 2.** High quality intact prairie-like scour community in Carter County in 2018. Note large pine tree, herbaceous community, and lack of cobble.



**Image 3.** Same spot as Image 2 — note same pine tree — in 2022 after a hot prescribed fire that consumed the thin soil. Note absence of herbaceous community and increased cobble.



ing of wild organisms rather than promoting a better conscious awareness and compassion of the natural world; spend millions of dollars on prescribed fire programs that continue to degrade the systems we pretend to be helping, despite the evidence; refuse to regulate invasive species introductions; and continue to allow rampant and unregulated agricultural practices to poison our land, waters, and children. Not fixing these problems is often linked to protecting the interests of our most ruggedly deluded individuals at the expense of the realities of our collective ecological sensitivities. I do not mean to write this judgmentally, for these are demonstrable facts. As such, “natural” more closely resembles mythology than reality, and we don’t ever talk about transcending this inadequate awareness.

The very concept of management is too heavy-handed. It is the ecological equivalent of mansplaining and evangelizing. Instead, we need to work within systems on a site-by-site basis. We need to spend hours, days, weeks just sitting, listening, and observing. We need to slow down and catch the beat. We need to find our own nature by meditating in nature before we act. We need to know what species are there, what those species require, and how to best meet the community building goals of connecting and perpetuating truly functional biodiversity in functional and perpetual expressions. We need people that understand this—that understand that anything short of this is destined by the laws of physics to fail. Compromise can fit into this, but we need practitioners that understand that physiology means ecology, that psychology means ecology, that chemistry means ecology, that patience means ecology. Ecology doesn’t mean rote burning. It doesn’t mean spraying. It doesn’t mean thinning. It doesn’t mean forestry mulch-

ing. It doesn’t mean grazing. It doesn’t mean any of the things we force upon ecology from farming, agriculture, industry, landscaping, etc. It means honoring system complexity and sacredness by transcending our own hubris and ignorance in a conscious way rather than as a hopeful accident. It means asking living systems what they need from us by understanding their intentions and working with their potential. It means patience and suffering with systems, not taking shortcuts and catering restoration to human cultural devices and constructs. It means a handlens and camera instead of a bulldozer and a can of poison. It means being different people than we are now because we know it doesn’t get fixed until we fix ourselves. All other threats are subordinate. 🌿

---

Justin Thomas is the Director of NatureCite

Contact: [justin.thomas@naturecite.org](mailto:justin.thomas@naturecite.org)



**Image 4.** Recently bulldozed high-quality prairie remnant on Highway 13 in Polk County.

# The Long-Term Impacts of Deer Herbivory in Determining Temperate Forest Stand and Canopy Structural Complexity

by Samuel P. Reed, Alejandro A. Royo, Alexander T. Fotis, Kathleen S. Knight, Charles E. Flower and Peter S. Curtis

*Editor's note:* The following is a reprint of an article from the Journal of Applied Ecology (with permission) regarding white-tailed deer impacts to forest canopy structure and composition in northern Pennsylvania. While it is widely known that Missouri ecosystems are vastly divergent from the structure and composition of forests in the Allegheny region of the northeastern states, similar impacts to forest canopies from deer overbrowse can be found in Missouri ecosystems. Deer overbrowse can result in a simplification of native flora as documented in research in the Midwest<sup>1</sup> and in Missouri State Parks during studies conducted in the mid-1990s<sup>2</sup>. Missouri's deer herd is estimated at 1.5 million individuals. With the development of natural spaces into urbanized communities, the pressure of deer browse on native flora becomes a topic worthy of investigating, and one that guides Missouri State Parks annually for requesting managed deer hunts to maintain sustainable deer numbers in state parks.

The article below follows a deer study for 36+ years, providing a significant data set and valuable information that may help guide land managers in Missouri on how to protect natural resources coincident with deer management.

1 Côté, S. D., Rooney, T. P., Tremblay, J., Dussault, C., & Waller, D. M. (2004). "Ecological Impacts of Deer Overabundance." *Annual Review of Ecology, Evolution & Systematics*, 35 (1), 113–147. <https://corescholar.libraries.wright.edu/biology/43>

2 Wiggers, Ernie P. "Deer in Missouri State Parks Survey. 1987-1998." University of Missouri. Unpublished MDNR Reports, Natural History Section.

## 1. INTRODUCTION

Forests are influenced by a variety of disturbances, which can have different effects on species composition, successional trajectories, and structure. Forest structure refers to the horizontal and vertical arrangement of vegetation and empty space in a stand—the height of the canopy, whether understories, midstories, and overstories are dense or open, and how that density varies spatially—which impacts carbon sequestration (Gough et al., 2019), wildlife habitat (Fotis et al., 2020), and other important attributes of ecosystem function (Fahey et al., 2018; Mori et al., 2017). Although pulse disturbances (e.g. short-term events that place high pressure on a system, such as windstorms or fire) can transform a stand's structure in minutes, press disturbances (e.g. long-term events that place continuous pressure on a system, such as intense herbivory or certain pathogens) operate continuously over years to decades across a landscape to significantly alter forest structural characteristics and associated ecosystem services (Flower & Gonzalez-Meler, 2015; Graham et al., 2021; Lake, 2000).

Ungulate browsing is a dominant press disturbance in forests worldwide that places consumptive pressure on preferred vegetation, shifting species composition by reducing seedling abundance and diversity, and slowing the pace towards late successional communities (Bernes et al., 2018). In eastern North America, white-tailed deer *Odocoileus virginianus* are the dominant ungulate browser and have a

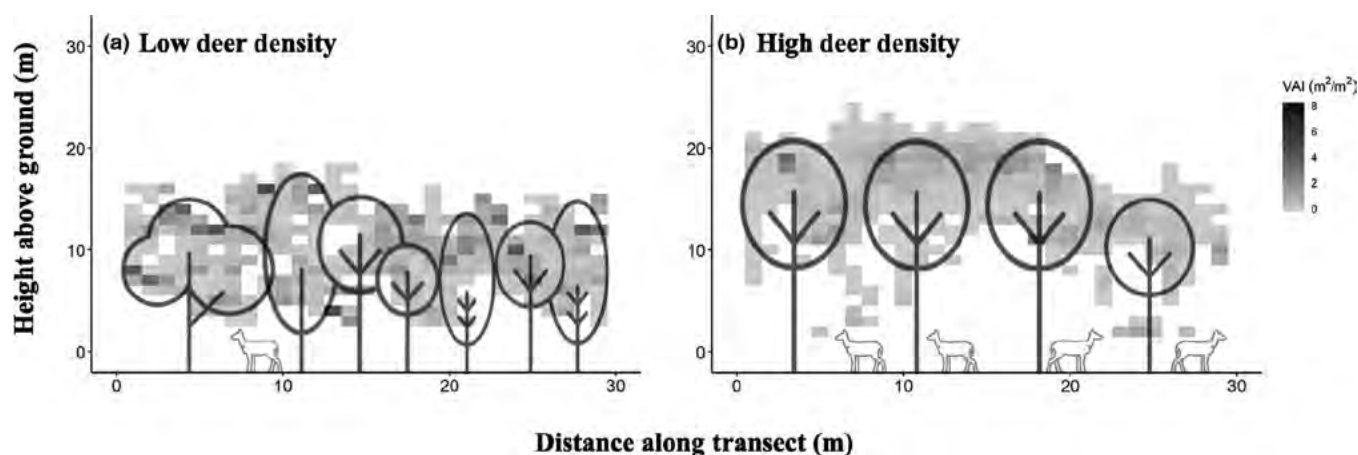


pronounced effect on early successional forest communities where vegetation is concentrated in shorter, more browse vulnerable size classes (Côté et al., 2004; Tilghman, 1989). Deer induced changes in vegetation early in stand development can transform successional trajectories and have long-term ramifications for the future forest's structure and thus, ecosystem function and services (Rooney & Waller, 2003).

Changes in forest structure may not be discernible until the regenerating tree community grows beyond the herbivory filter, a process which accrues over decades (Weisberg & Bugmann, 2003). The influence of vertebrate herbivores on stand structural metrics such as diameter at breast height (DBH) or tree density has received considerable attention (Ramirez et al., 2018; White, 2012). For example, Hidding and colleagues (2013) found that high white-tailed deer browse pressure transformed regenerating boreal forest communities into open spruce (*Picea* spp.) savannas after 15 years, whereas complete or partial protection from browsing allowed the development of a dense young forest characterized by hardwoods and conifers. Similarly, in the Appalachian-Northern hardwood forests of the eastern United States, long-term browsing created understories dominated by striped maple *Acer pensylvanicum*, a subcanopy treelet, while long-term elimination of browsing led to a more diverse understory community (Kain et al., 2011). Shifts in tree community composition or a species' dominance could then lead to collapses in canopy structure since many trees have species-specific crown architectures that contribute to canopy arrangement (Pretzsch, 2014). Although there is evidence of disturbances such as ice storms, forest pathogens, and fire leaving a unique mark on temperate forest canopies (Atkins et al., 2020; Fahey et al., 2016), very few studies identify the effects of long-term vertebrate herbivory on canopy

structure (Côté et al., 2004; Nuttle et al., 2011). To our knowledge, only one study has quantified deer density impacts on a mature forest's canopy height, finding that increased deer populations led to taller canopies in Britain (Eichhorn et al., 2017). Nevertheless, herbivore impacts on canopy structure remain understudied and elusive due to a lack of operational and accessible technologies to quantify canopy structural metrics. To make field-based, observational insights on the relationships between herbivores and canopy structure, researchers must possess tools that permit simple and reliable quantification of post-disturbance canopy structural metrics for vegetation strata that are far taller than the observer (Ritchie et al., 1993).

In this study, we capitalize on a controlled browsing experiment initiated in 1979–1980 on the Allegheny Plateau, USA, where forests regenerated under four controlled white-tailed deer densities for 10 years (Tilghman, 1989). We use a Portable Canopy LiDAR (PCL) system to rapidly characterize deer-induced changes in canopy structure in these now 36-year-old stands (Figure 1, next page). While PCL has been used to measure canopy structural complexity of temperate forests in light of several disturbances (Atkins et al., 2020; Fahey et al., 2016; Hardiman et al., 2013), this technology has not been applied to study the influence of deer browse, the eastern North American forest's dominant press disturbance. This controlled browsing experiment, using deer enclosures rather than exclosures, has only been replicated once, in the boreal forests of Quebec, Canada (Tremblay et al., 2007). These experimental stands provide a unique opportunity to examine the legacy of deer browse pressure during stand initiation on forest canopy structure after nearly four decades of growth, during which stratification has occurred and stems of species that will characterize the main canopy for the next several decades are



**Figure 1.** Example of a ‘hit grid’ showing different canopy structures between low and high deer density treatments, as measured by the portable canopy LiDAR system. The tree silhouettes represent a hypothetical stand and canopy structure based on the LiDAR returns. Darker bins indicate greater laser return density and increased canopy foliage (VAI: vegetative area index), with data processed in the *forestr* package (Atkins, Bohrer, et al., 2018). Figure 1a is representative of the more diverse and dense canopies associated with the low deer density treatments (Gap Fraction: 1.4%; VAI: 7.2; Rugosity 4.1; Mean Max Height: 14.9), whereas Figure 1b is representative of the open, savanna-like stands of black cherry associated with high deer densities (Gap Fraction: 14.3%; VAI: 4.8; Rugosity: 8.6; Mean Max Height: 19.3) (Trees from Made by Made & Deer from Berkah Icon; The Noun Project)

established (Hibbs, 1983). In this work, our primary goal is to assess the impacts of varying deer density during stand initiation on (a) long-term forest species diversity, composition, and stand structure, and (b) long-term canopy complexity.

## 2. MATERIALS AND METHODS

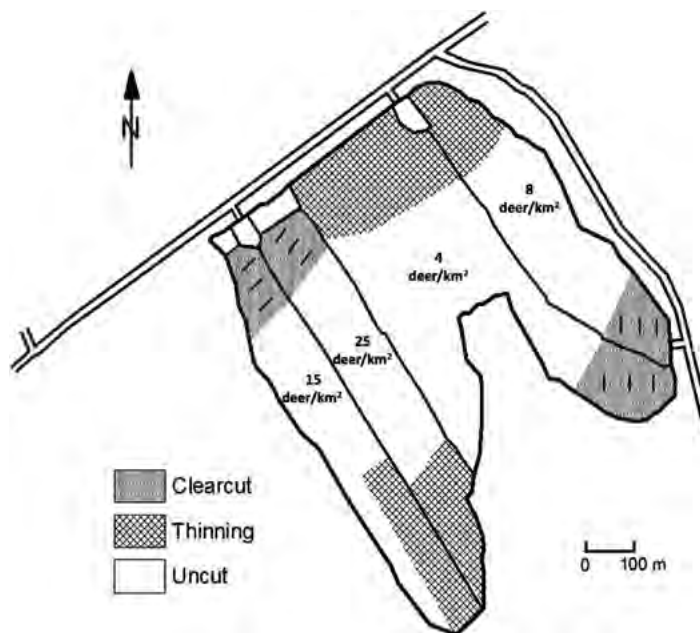
### 2.1 STUDY SITE AND DESIGN

This experiment took place at four sites within the Allegheny Plateau Region of north-western and north-central Pennsylvania, USA. Sites were distantly located in Elk County (710 m elevation; 41°34'22"N, 78°28'30"W), Warren County (550 m elevation; 41°38'48"N, 79°08'11"W), Forest County (550 m elevation; 41°34'40"N, 79°06'19"W), and McKean County (670 m elevation; 41°38'21"N, 78°19'33"W; Horsley et al., 2003). Each location was composed of 60- to 70-year-old second-growth stands of black cherry *Prunus serotina*, red maple *Acer rubrum*, and sugar maple *Acer saccharum* prior to the establishment of the experimental treatments (Tilghman, 1989). Within the four sites, a 65 ha deer enclosure with 2.5 m high fencing was assembled. Two enclosures were established in 1979 and the other two enclosures in 1980, each constructed and

operated in direct consultation with the Pennsylvania Game Commission through designation of all sites as State Game Propagation Areas. Each 65 ha site was subdivided with fencing to establish experimental manipulations of deer populations at densities of 4, 8, 15, and 25 deer/km<sup>2</sup>, for a total of four replicates of each density treatment (Figure 2; Tilghman, 1989). The lowest deer density treatments (4 deer/km<sup>2</sup>) were 26 ha, whereas the rest of the stands were 13 ha. Nested within each deer density treatment were three different overstorey conditions: clearcut, cut to 60% residual relative density, and uncut. Clearcuts represented 10% of each deer density treatment's area (1.3 or 2.6 ha). We considered only the clearcut areas in this study as the entire stand was re-initiated and deer had a direct influence on all trees currently in the overstorey. All enclosures were disassembled in 1990, after which deer could travel unimpeded. One treatment (15 deer/km<sup>2</sup>) at State Game Land 30 was harvested prior to our study, reducing our sample size to 15 treatment areas. For a more detailed description of the experimental design, initial conditions, and vegetative trajectories, see Horsley et al. (2003).



**Figure 2.** Map of one of four deer enclosures showing the different deer density and forest management treatments with each line in the clearcut location representing a 30 × 5 m belt transect. Deer populations were maintained for approximately 10 years within the enclosure experiment (1989–1990). This study evaluated stand and canopy structure in the clearcut sections of each deer density treatment



## 2.2 FOREST SPECIES DIVERSITY, STAND STRUCTURE, & CANOPY STRUCTURAL COMPLEXITY

In June and July 2016, we measured forest stand structure, species composition, and canopy structure, approximately 36 years after stand re-initiation and deer browsing. All field work was conducted with an approved study plan and memoranda of understanding between participating landowners. Within each deer density treatment, we randomly placed three, 30 × 5 m parallel belt transects spaced at least 30 m away from one another. Within each transect, we identified and measured the diameter at breast height (DBH) of all trees >5 cm DBH. From DBH, basal area was calculated at the transect level (150 m<sup>2</sup>) and then extrapolated to a per hectare basis (10,000 m<sup>2</sup>). Shannon diversity was calculated with basal area as the unit of abundance using R package VEGAN (Oksanen et al., 2020).

Canopy structural complexity was measured using a ground-based portable canopy LiDAR system (PCL; Parker et al., 2004). The PCL measures the arrangement of leaves and branches within a canopy using an upward-facing infrared laser at 2,000 Hz and is an economical means to rapidly collect and calculate multiple, high-resolution canopy structural metrics at the stand

scale. Canopy structural metrics were calculated using the FORESTR R package (Atkins, Bohrer, et al., 2018). Although FORESTR can calculate nearly two dozen canopy structural parameters, we focused on metrics that characterize four different aspects of canopy structural complexity and are commonly studied in relation to disturbance; vegetation area index (VAI; the density of vegetation within the canopy, or the density of LiDAR returns within each 1 × 1 m column along PCL transect), mean outer canopy height (MOCH; average maximum return height of lasers along transect), gap fraction (the openness of the canopy, or the ratio of PCL sky hits to vegetation returns), and rugosity (canopy structural complexity, or the vertical and horizontal heterogeneity in leaf, branch and stem distributions; Atkins, Bohrer, et al., 2018; Atkins et al., 2020). These metrics correlate well with important ecophysiological responses including above-ground primary productivity (ANPP, Fotis et al., 2018; Hardiman, Gough, et al., 2013) and leaf traits (Fotis & Curtis, 2017), and can characterize habitat heterogeneity features that predict wildlife diversity (e.g. Ishii et al., 2004; avian diversity, Seavy et al., 2009; squirrel habitat, Fotis et al., 2020).

Canopy metrics				
Treatment	VAI (m <sup>2</sup> /m <sup>2</sup> )	MOCH (m)	Gap fraction (%)	Rugosity (m)
4 deer/km <sup>2</sup>	7.53 ± 0.07a	13.68 ± 0.70	0.81 ± 0.23a	7.40 ± 0.80ab
8 deer/km <sup>2</sup>	7.34 ± 0.18a	12.09 ± 0.46	0.90 ± 0.26a	5.85 ± 0.49b
15 deer/km <sup>2</sup>	7.62 ± 0.12a	12.32 ± 0.64	0.65 ± 0.22a	9.01 ± 0.70a
25 deer/km <sup>2</sup>	6.17 ± 0.25b	14.96 ± 1.15	4.70 ± 1.35b	8.72 ± 0.92a
Effect	<b>F3,17.2 = 9.45;</b> <b>p = 0.0007</b>	<b>F3,3.2 = 3.97;</b> <b>p = 0.0505</b>	<b>F3,39.6 = 8.02;</b> <b>p = 0.0003</b>	<b>F3,18.3 = 7.98;</b> <b>p = 0.0013</b>

Stand metrics				
Treatment	Richness (S)	Stem density (N/ha)	Basal area (m <sup>2</sup> /ha)	Diversity (H')
4 deer/km <sup>2</sup>	4.67 ± 0.22	2,487 ± 191a	36.14 ± 1.89a	1.17 ± 0.14a
8 deer/km <sup>2</sup>	5.25 ± 0.29	2,210 ± 106ab	27.64 ± 1.89bc	1.25 ± 0.14a
15 deer/km <sup>2</sup>	4.56 ± 0.63	2,550 ± 178a	34.94 ± 2.27ab	0.91 ± 0.15ab
25 deer/km <sup>2</sup>	3.92 ± 0.60	1,721 ± 191b	25.78 ± 1.89c	0.73 ± 0.14b
Effect	<b>F3,16.7 = 1.51;</b> <b>p = 0.2474</b>	<b>F3,18.1 = 3.80;</b> <b>p = 0.0284</b>	<b>F3,39.4 = 6.44;</b> <b>p = 0.001</b>	<b>F3,38.4 = 6.43;</b> <b>p = 0.0012</b>

**Table 1.** (top) Canopy complexity metrics (VAI, Mean Outer Canopy Height, Gap Fraction, Rugosity). (bottom) Stand metrics (Species Richness, Stem Density, Basal Area, Shannon Diversity) of trees as measured in 2016 within the clearcut sections of deer density treatments on the Allegheny Plateau

### 2.3 STATISTICAL ANALYSIS

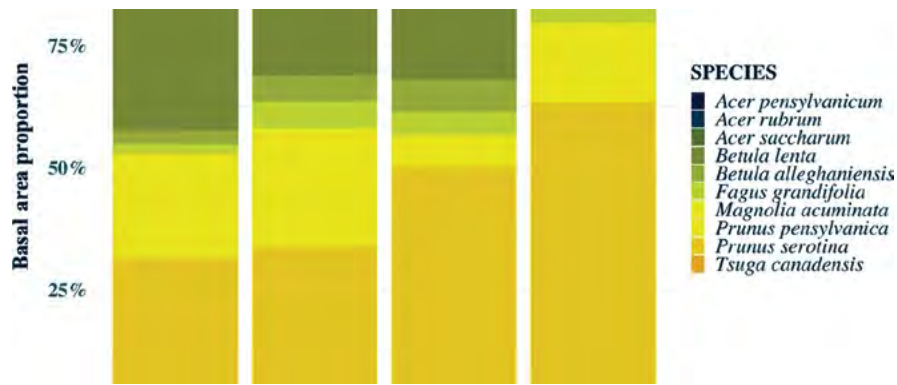
We used analysis of variance (ANOVA) to assess treatment effects on stand structural attributes, species diversity, and canopy structural metrics using general linear mixed models (Proc GLIMMIX; SAS 9.4, SAS Institute, Inc.). Our experiment is a nested randomized complete block design where deer density is considered a fixed effect and both site and transect are considered random effects. This design assumes independent transects nested within each deer density treatment. This is modelled on Nuttle and colleague's (2014) approach within the same experiment and is reasonable given that tree basal area was low and distance between transects ( $\geq 30$  m) was large, which likely exceeds direct canopy interaction distance between each transect (Lorimer, 1983). We tested this assumption by running exploratory analyses that modeled spatial autocorrelation among transects using a second, spatial power random effect. These models either had poorer

fit (i.e. higher AICc) or failed to converge, and did not change interpretation, suggesting spatial autocorrelation was minimal (See Appendix Tables S1 and S2<sup>1</sup>). Nevertheless, we present those results so the reader can draw their own conclusions about potential spatial dependence.

Normality was tested using the Shapiro–Wilk test. Vegetation area index, rugosity, basal area, and tree species diversity (H') were normally distributed. Gap fraction, MOCH, DBH, species richness, and stem density were right-skewed. For these, continuous response variables were modeled using a gamma distribution, whereas count data used Poisson (richness) or negative binomial distribution (stem density). We graphically examined the normality of the residuals, tested the homogeneity of the variance using boxplots and Levene's tests. Where necessary, this residual variance was adjusted using a second random statement with a 'group=' option. All models used a Kenward–Roger denominator

<sup>1</sup> <https://doi.org/10.1111/1365-2664.14095>





**Figure 3.** Proportional breakdown of species by basal area within each deer density treatment. As deer densities increase, so does the canopy dominance of unpalatable black cherry *Prunus serotina* (orange), while more shade-tolerant species decrease

degrees of freedom adjustment method. Where a significant (critical value = 0.05) deer density treatment effect was detected, we tested pairwise differences among deer density treatments with the LSMEANS function statement and used the Tukey–Kramer adjustment for multiple comparisons (Lenth, 2016).

### 3. RESULTS

#### 3.1 STAND DIVERSITY, COMPOSITION AND STRUCTURE

We found a significant decrease in the Shannon diversity of tree species with increased deer density ( $p = 0.001$ ,  $F = 6.43$ , Table 1 previous page) nearly 36 years after the initiation of the enclosure experiment, wherein the highest deer density treatments (15 and 25 deer/km<sup>2</sup>) were relatively depauperate and dominated by black cherry *Prunus serotina*. The lowest deer density

treatments had greater representation of pin cherry *Prunus pensylvanica*, red maple *Acer rubrum*, and birch *Betula* spp. as well as black cherry (Figure 3; Table 2). Across deer density treatments, black cherry’s proportional abundance steadily increased with greater deer browse pressure (4 deer/ km<sup>2</sup> = 15.6%, 8 deer/km<sup>2</sup> = 18.4%, 15 deer/ km<sup>2</sup> = 39.5%, 25 deer/ km<sup>2</sup> = 60.4%), being the highest at the 25 deer/km<sup>2</sup>, whereas the proportional abundance of all other species generally decreased (Table 2). While average species richness was also low at the 15 and 25 deer/km<sup>2</sup> treatment, there were no significant differences in richness among density treatments ( $p = 0.25$ ,  $F = 1.51$ , Table 1; see also Tilghman, 1989). Stem density and basal area also decreased at the highest deer density. Stem density was highest at 4 and 15 deer/ km<sup>2</sup>, had a moderate decrease

**Table 2.** Tree species density and proportional abundance by deer density treatment (APCE = *Acer pensylvanicum*; ACRU = *Acer rubrum*; BELEN = *Betula lenta*; BETAL = *Betula alleghaniensis*; FAGR = *Fagus grandifolia*; MAGAC = *Magnolia acuminata*; PRPN = *Prunus pensylvanica*; PRSR = *Prunus serotina*). Species that did not appear in more than two density treatments (*Tsuga canadensis* and *Acer saccharum*) were not included

Treatment	Species density (N/ha)								Total
	ACPE	ACRU	BELEN	BETAL	FAGR	MAGAC	PRPN	PRSR	
4 deer/ km <sup>2</sup>	17 (0.7%)	211 (8.5%)	1006 (40.5%)	94 (3.8%)	172 (6.9%)	22 (0.9%)	567 (22.8%)	389 (15.6%)	2,487
8 deer/ km <sup>2</sup>	6 (0.3%)	394 (17.8%)	489 (22.1%)	100 (4.5%)	344 (15.6%)	11 (0.5%)	461 (20.9%)	406 (18.4%)	2,210
15 deer/ km <sup>2</sup>	15 (0.6%)	163 (6.4%)	652 (25.6%)	141 (5.5%)	400 (15.7%)	7 (0.3%)	89 (3.5%)	1007 (39.5%)	2,550
25 deer/ km <sup>2</sup>	17 (1.0%)	61 (3.5%)	133 (7.7%)	78 (4.5%)	178 (10.3%)	0	217 (12.6%)	1039 (60.4%)	1,721

at 8 deer/km<sup>2</sup> and then was significantly lower than every other treatment at 25 deer/km<sup>2</sup> ( $p = 0.03$ ,  $F = 3.80$ , Table 1). Basal area was highest at 4 deer/km<sup>2</sup> and 15 deer/km<sup>2</sup>, moderately lower at 8 deer/km<sup>2</sup>, and lowest at 25 deer/km<sup>2</sup> ( $p = 0.001$ ,  $F = 6.44$ , Table 1). Both metrics varied with intermediate deer browsing but were consistently the lowest within the 25 deer/km<sup>2</sup> treatment.

### 3.2 CANOPY STRUCTURE

The highest deer density treatment also had significant effects on canopy complexity. Stands established at the highest browsing levels showed the lowest VAI ( $p < 0.001$ ,  $F = 9.45$ , Table 1). There were no significant differences in VAI between the 4, 8 or 15 deer/km<sup>2</sup> stands. There was a concomitant increase in gap fraction for canopies in the 25 deer/km<sup>2</sup> treatment ( $p < 0.001$ ,  $F = 39.64$ , Table 1), but little difference in this metric between the 4, 8 and 15 deer/km<sup>2</sup> treatments. Both VAI and gap fraction were strongly negatively correlated with one another and are treated as corresponding variables in the discussion ( $r = -0.92$ , Appendix Figure S1).

Rugosity, a measure of the heterogeneity in vertical and horizontal leaf, branch and stem distribution, showed substantial variation among deer density treatments. Rugosity was highest at 15 and 25 deer/km<sup>2</sup>, lowest at 8 deer/km<sup>2</sup>, and intermediate in the 4 deer/km<sup>2</sup> treatment ( $p = 0.001$ ,  $F = 7.98$ , Table 1). Mean outer canopy height also varied among treatments, with trees in the 4 and 25 deer/km<sup>2</sup> treatments being an average of 1–3 m taller than trees in the 8 and 15 deer/km<sup>2</sup> treatments ( $p = 0.051$ ,  $F = 3.97$ , Table 1).

---

## 4. DISCUSSION

---

The legacy of deer browse is still widely apparent in the experimental forest's species composition, stand structure, and canopy structural complexity, despite the deer density treatments having ended nearly three decades ago. As deer are present at high densities throughout

eastern North American forests, our results indicate that this severe press disturbance can have a dramatic influence on forest structure at multiple levels for many years.

High deer density at stand initiation led to low tree diversity in the overstorey, with black cherry being the dominant canopy species (Figure 3; Table 2). These results contribute to extensive literature showing that high deer browsing results in low plant diversity (Goetsch et al., 2011; Habeck & Schultz, 2015; Russell et al., 2017). Our observation that high deer densities favor black cherry growth is also supported by Royo et al. (2021) and by prior studies in stand development within our experiment (Horsley et al., 2003; Nuttle et al., 2011; Tilghman, 1989), further demonstrating the persistent legacy of deer browsing on stand diversity. Black cherry, being cyanogenic, is unpalatable to deer, making it one of the primary tree species to survive following the intense browse pressure in the 25 deer/km<sup>2</sup> treatment (Horsley et al., 2003). Other ecologically and economically valuable tree species, such as maple and birch, remain in low abundance in the 25 deer/km<sup>2</sup> treatments after 36 years (Figure 3).

High deer density treatments had low tree density and basal area as well, similar to the results of Horsley et al. (2003) who found that increasing deer density reduced stem density 5 years post-treatment. However, this browse effect on tree density was not observed by Nuttle et al. (2011) at 10- and 25-year post-treatment, who found little difference in tree density between treatments. They hypothesized that low-palatability species, such as black cherry, were able to regenerate and fill niche space of high-palatability species, consistent with Leibold's edibility hypothesis (Leibold, 1989; Nuttle et al., 2011). We suggest that over time, high deer densities at our site led to a recalcitrant understorey, with unpalatable hay-scented fern *Dennstaedtia punctilobula*



spreading during stand initiation and eventually dominating the understorey of most of the 25 deer/km<sup>2</sup> stands (Nuttle et al., 2014). As these stands began self-thinning, the fern understorey prevented tree regeneration through shading

and resource competition, as has been seen in other parts of Pennsylvania (Royo & Carson, 2006). The legacy effect of deer browse on tree density we observed has therefore likely re-emerged due to compositional differences in the regeneration layer among treatments, whereby a recalcitrant understorey prevented further tree regeneration following the self-thinning of uneaten, shade intolerant black cherry in high deer density areas. These results underscore the importance of long-term monitoring of stands afflicted by deer browse (or other press disturbance agents), as the effects of herbivory on stand structure may take decades to fully develop. Furthermore, these sparse black cherry stands at 25 deer/km<sup>2</sup> had the lowest basal area and thus, the lowest above-ground biomass, as both metrics are highly correlated ( $r = 0.99$ ; Appendix Table S3). Low tree basal area at the highest deer density indicates that overabundant herbivore populations can cause reductions in above-ground carbon stocks over time through species community change (White, 2012).

The combination of changes in tree species composition and stand structure in the highest deer density treatment translated into changes in canopy structure: a stark decrease in VAI and increase in canopy gap fraction at 25 deer/km<sup>2</sup>. Functionally, this implies a reduction in the density and connectivity of canopy leaves, with foliage now highly aggregated and clustered around black cherry stems (Figure 1). This finding aligns with Canham et al. (1994) who found that black cherry had the lowest crown depth (the proportion of tree height to tree-crown depth) of many common temperate tree species and Sullivan et al. (2017) who found that

shade intolerant species have narrower canopies. The deer browse effect on crown geometries and canopy structure, as quantified with the PCL, may also signal the beginning of a shift in forest structure to an alternative state, one described by Stromayer and Warren (1997) as a 'deer savanna'. In our system, high deer browse pressure caused significant changes in species composition, gap fraction, and VAI, with black cherry dominating the overstorey and hay-scented fern dominating the understorey.

The impact of deer on VAI presented herein is more similar to pulse disturbances, such as fire and ice storms, than press disturbances, such as acid rain or some pathogens. Deer, fire, and ice storms each reduce canopy VAI through species compositional changes, leaf combustion, or stem collapse, respectively (Atkins et al., 2020; Fahey et al., 2020). In contrast, acidification and pathogens such as hemlock woolly adelgid have shown relatively little influence on VAI, potentially because these slow-acting disturbances allow for foliar replacement in the canopy over time (Atkins et al., 2020). However, the impact of herbivory on canopy vegetative density is likely to be longer-lasting than a single fire or ice storm event. Deer have changed the stand's VAI through lasting shifts in species composition and canopy architecture rather than through moderate canopy combustion or breakage, which likely only have a short temporal signature. These long-term reductions in canopy density by deer can then influence ecological function, as VAI is strongly correlated with the fraction of photosynthetically active radiation (fPAR) absorbed by the canopy (Atkins et al., 2018) and influences wildlife such as arthropods, bird species, reptiles, and other arboreal species (Cuddington, 2011; Nuttle et al., 2011; Ulyshen, 2011).

Rugosity showed less straightforward treatment responses. The increase in rugosity associated with higher deer densities and gap fraction is similar to Fotis et al. (2018) who found that stands with low stem densities had more open canopies and greater horizontal variability, which contributes to greater rugosity. Since all of our stands are still in the stem exclusion phase, stands in the low deer density treatment are dense and less horizontally complex than stands in the high deer density treatment, causing a difference in rugosity. Our findings are consistent with the canopy structural classification system of Fahey et al. (2019), where dense forests in the stem exclusion phase have low rugosity and young, patchy canopies have slightly higher rugosity.

Other temperate forest disturbances have had variable influences on rugosity. Ice storms, hemlock wooly adelgid, and now white-tailed deer browse increase rugosity, age-related senescence decreases rugosity, while fires, historic logging, beech bark disease, and acidification have little effect (Atkins et al., 2020; Wales et al., 2020). The variable response of rugosity to disturbance type indicates that multiple canopy structural metrics should be considered to gain a more holistic perspective on which aspect(s) of the canopy change. As our stands continue to develop, rugosity could become a useful metric to predict NPP in light of herbivory disturbance, as it is strongly correlated with greater net primary productivity within maturing stands (Gough et al., 2019, 2021). Furthermore, since stand age and time since disturbance are of particular importance when measuring rugosity, but are often difficult to standardize across studies, long-term experimental studies such as ours are particularly important to better understand these disturbance–canopy interactions (Wales et al., 2020).

We found that tree canopies were tallest at the lowest (4 deer/ km<sup>2</sup>) and highest (25 deer/km<sup>2</sup>)

deer density treatments. This pattern may have been driven by differences in preferred browse species at each end of the deer density spectrum, with palatable pin cherry favored at 4 deer/ km<sup>2</sup> and unpalatable black cherry at 25 deer/ km<sup>2</sup> (Figure 3; Table 2). Both *Prunus* species are shade intolerant and fast growing, making the low and high deer density canopies taller than those dominated by more shade-tolerant species such as beech, maple and birch (Table 1; Figure 3; Canham et al., 1994). Differences in canopy height and composition could influence each stand's total above-ground biomass and ability to support various wildlife habitat types (Fotis et al., 2020; Seavy et al., 2009; Sullivan et al., 2017; Wang et al., 2021). These results support other studies showing that press disturbances can have a positive impact on MOCH through species-specific influences. For instance, soil acidification likely increases MOCH by favoring upper canopy growth and loss of subcanopy species (Atkins et al., 2020). Eichhorn et al. (2017) found that increased deer densities led to taller canopies in southern England, although the mechanism for this effect was unclear. Our experiment provides clear evidence that high deer densities impact canopy height decades after stand establishment by altering the relative abundance of tree species that vary in shade tolerance and growth rate. Such species-specific influences by press disturbances may be an important mechanism affecting changes in canopy height and structure.

Effective management of forest structure and canopy complexity in light of current or future disturbances is becoming a priority due to structure's many connections to ecosystem function and resilience (Fahey et al., 2018; Seidl et al., 2016). Using a PCL, we have gained insight on how a decade of deer browse disturbance can leave a distinct signal on the canopy, with high deer density leading to high rugosity, gap fraction, and canopy height, with low VAI. Since



ungulates are at high densities in many forests globally, our work provides a basis for generalizing how intense herbivory may affect key canopy structural traits over time (Bernes et al., 2018). By allowing ungulate populations to remain at high densities, forest managers are indirectly changing stand and canopy structure, which likely has important long-term ramifications on many associated ecosystem functions. Therefore, long-term monitoring of canopy structure in forests with heavily managed ungulate populations could serve as an indicator of both ecological function and management success (Gatica-Saavedra et al., 2017).

## 5. CONCLUSIONS

Using a long-term deer enclosure experiment, our study is the first to apply a PCL system to determine how varying deer densities affect canopy structure. We show that deer leave a unique legacy on the structure of northern hardwood forests at multiple levels, from species diversity to canopy complexity, and that these changes can be detected with the PCL. Over three decades after the conclusion of the experimental treatments, at the highest deer density treatment we saw decreases in tree diversity, basal area, tree density, canopy VAL, and increases in gap fraction and rugosity. Furthermore, we found that tree density and basal area varied widely with different deer browse intensities due to changes in species composition and that these effects of deer browse may take decades to become fully pronounced. Although the influence of herbivory is pervasive across many forest types (Bernes et al., 2018; Patton et al., 2018), there has been little prior quantitative evidence of the legacy of browsing pressure on canopy structure in temperate forests. Deer herbivory may be one of the most important drivers of forest composition and canopy structure over long time-scales, which could have significant

ramifications on wildlife habitat (Fotis et al., 2020), carbon sequestration and storage (Fotis et al., 2018; Gough et al., 2020; Hardiman et al., 2011), light-use efficiency (Atkins, Fahey, et al., 2018; Hardiman, Gough, et al., 2013), and timber extraction (Miller et al., 2009) in the present and into the future. 🌳

Samuel P. Reed is with the Department of Forest Resources at the University of Minnesota, St. Paul, Minnesota

Alejandro A. Royo is with the Forestry Sciences Lab, USDA Forest Service, Northern Research Station, Irvine, Pennsylvania

Alexander T. Fotis, Kathleen S. Knight, Charles E. Flower are with the USDA Forest Service, Northern Research Station, Delaware, Ohio

Peter S. Curtis is Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio

### References

- Atkins, J. W., Bohrer, G., Fahey, R. T., Hardiman, B. S., Morin, T. H., Stovall, A. E. L., Zimmermann, N., & Gough, C. M. (2018). Quantifying vegetation and canopy structural complexity from terrestrial LIDAR data using the forster R package. *Methods in Ecology and Evolution*, 9(10), 2057–2066. <https://doi.org/10.1111/2041-210X.13061>
- Atkins, J. W., Bond-Lamberty, B., Fahey, R. T., Haber, L. T., Stuart-Haëriens, E., Hardiman, B. S., LaRue, E., McNeil, B. E., Orwig, D. A., Stovall, A. E. L., Tallant, J. M., Walter, J. A., & Gough, C. M. (2020). Application of multidimensional structural characterization to detect and describe moderate forest disturbance. *Ecosphere*, 11(6), e03356. <https://doi.org/10.1002/ecs2.356>
- Atkins, J. W., Fahey, R. T., Hardiman, B. S., & Gough, C. M. (2018). Forest canopy structural complexity and light absorption relationships at the subcontinental scale. *Journal of Geophysical Research: Biogeosciences*, 123(4), 1387–1405. <https://doi.org/10.1002/2017JG004356>
- Bernes, C., Macura, B., Jonsson, B. G., Junninen, K., Müller, J., Sandström, J., Löhmus, A., & Macdonald, E. (2018). Manipulating ungulate herbivory in temperate and boreal forests: Effects on vegetation and invertebrates. A systematic review. *Environmental Evidence*, 7(1), 3. <https://doi.org/10.1861/ISS30-018-01253>
- Canham, C., Finzi, A., Pacala, S., & Burbank, D. (1994). Causes and consequences of resource heterogeneity in forests: Interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, 24(2), 337–349. <https://doi.org/10.1891/1924-046>
- Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 113–147. <https://doi.org/10.1146/annurev.ecolsys.35.021003.105725>
- Cuddington, K. (2011). Legacy effects: The persistent impact of ecological interactions. *Biological Theory*, 6(3), 203–210. <https://doi.org/10.1007/s13752-012-0027-5>
- Eichhorn, M. P., Rydberg, J., Smith, M. J., Gill, R. M. A., Sirwardena, G. M., & Fuller, R. J. (2017). Effects of deer on woodland structure revealed through terrestrial laser scanning. *Forest Ecology and Management*, 394(6), 165–1626. <https://doi.org/10.1016/j.foreco.2018.01.011>
- Fahey, R. T., Alveshery, B. C., Burton, J. I., D'Amato, A. W., Dickinson, Y. L., Keeton, W. S., Kern, C. C., Larson, A. J., Palik, B. J., Puettmann, K. J., Saunders, M. R., Webster, C. R., Atkins, J. W., Gough, C. M., & Hardiman, B. S. (2018). Shifting conceptions of complexity in forest management and silviculture. *Forest Ecology and Management*, 421, 59–71. <https://doi.org/10.1016/j.foreco.2018.01.011>
- Fahey, R. T., Atkins, J. W., Campbell, J. L., Rustad, L. E., Duffy, M., Driscoll, C. T., Fahey, T. J., & Schaberg, P. G. (2020). Effects of an experimental ice storm on forest canopy structure. *Canadian Journal of Forest Research*, 50(2), 136–145. <https://doi.org/10.1139/cjfr-2019-0276>

- Fahey, R. T., Atkins, J. W., Gough, C. M., Hardiman, B. S., Nave, L. E., Tallant, J. M., Nadehoffer, K. J., Vogel, C., Scheuermann, C. M., Stuart-Haëntjens, E., Haber, L. T., Fotis, A. T., Ricart, R., & Curtis, P. S. (2019). Defining a spectrum of integrative trait-based vegetation canopy structural types. *Ecology Letters*, 22(12), 2049–2059. <https://doi.org/10.1111/ele.13388>
- Fahey, R. T., Stuart-Haëntjens, E. J., Gough, C. M., De La Cruz, A., Stockton, E., Vogel, C. S., & Curtis, P. S. (2016). Evaluating forest subcanopy response to moderate severity disturbance and contribution to ecosystem-level productivity and resilience. *Forest Ecology and Management*, 376, 135–147. <https://doi.org/10.1016/j.foreco.2016.06.001>
- Flower, C. E., & Gonzalez-Meler, M. A. (2015). Responses of temperate forest productivity to insect and pathogen disturbances. *Annual Review of Plant Biology*, 66(1), 547–569. <https://doi.org/10.1146/annurev-arplant-043014-115540>
- Fotis, A. T., & Curtis, P. S. (2017). Effects of structural complexity on within-canopy light environments and leaf traits in a northern mixed deciduous forest. *Tree Physiology*, 37(10), 1426–1435. <https://doi.org/10.1093/treephys/tpw124>
- Fotis, A. T., Morin, T. H., Fahey, R. T., Hardiman, B. S., Bohrer, G., & Curtis, P. S. (2018). Forest structure in space and time: Biotic and abiotic determinants of canopy complexity and their effects on net primary productivity. *Agricultural and Forest Meteorology*, 250–251, 181–191. <https://doi.org/10.1016/j.agrformet.2017.12.251>
- Fotis, A. T., Patel, S., & Chavez, A. S. (2020). Habitat-based isolating barriers are not strong in the speciation of ecologically divergent squirrels (*Tamiasciurus douglasii* and *T. hudsonicus*). *Behavioral Ecology and Sociobiology*, 74(3), 32. <https://doi.org/10.1007/s00265-020-2814-5>
- Gatica-Saavedra, P., Echeverría, C., & Nelson, C. R. (2017). Ecological indicators for assessing ecological success of forest restoration: A world review. *Restoration Ecology*, 25(6), 850–857. <https://doi.org/10.1111/rec.12586>
- Goetsch, C., Wigg, J., Royo, A. A., Ristau, T., & Carson, W. P. (2011). Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: Results from a 60 year-old deer exclusion plot. *The Journal of the Torrey Botanical Society*, 138(2), 220–224. <https://doi.org/10.3159/TORREY-D-11-0003.1>
- Gough, C. M., Atkins, J. W., Bond-Lamberty, B., Agee, E. A., Dorheim, K. R., Fahey, R. T., Grigri, M. S., Haber, L. T., Mathes, K. C., Pennington, S. C., Shiklomanov, A. N., & Tallant, J. M. (2021). Forest structural complexity and biomass predict first-year carbon cycling responses to disturbance. *Ecosystems*, 24(3), 699–712. <https://doi.org/10.1007/s10021-020-00544-1>
- Gough, C. M., Atkins, J. W., Fahey, R. T., & Hardiman, B. S. (2019). High rates of primary production in structurally complex forests. *Ecology*, 100(10), e02864. <https://doi.org/10.1002/ecy.2864>
- Gough, C. M., Atkins, J. W., Fahey, R. T., Hardiman, B. S., & LaRue, E. A. (2020). Community and structural constraints on the complexity of eastern North American forests. *Global Ecology and Biogeography*, 29(12), 2107–2118. <https://doi.org/10.1111/geb.13180>
- Graham, E. B., Averill, C., Bond-Lamberty, B., Knelman, J. E., Krause, S., Peralta, A. L., Shade, A., Smith, A. P., Cheng, S. J., Fanin, N., Freund, C., Garcia, P. E., Gibbons, S. M., Van Goethem, M. W., Guebila, M. B., Kemppinen, J., Nowicki, R. J., Pausas, J. G., Reed, S. P., ... Zipper, S. C. (2021). Toward a generalizable framework of disturbance ecology through crowdsourced science. *Frontiers in Ecology and Evolution*, 9, 76. <https://doi.org/10.3389/fevo.2021.588940>
- Habeck, C., & Schultz, A. (2015). Community-level impacts of white-tailed deer on understory plants in North American forests: A meta-analysis. *AoB Plants*, 7. <https://doi.org/10.1093/aobpla/plv119>
- Hardiman, B. S., Bohrer, G., Gough, C. M., & Curtis, P. S. (2013). Canopy structural changes following widespread mortality of canopy dominant trees. *Forests*, 4(3), 537–552. <https://doi.org/10.3390/f4030537>
- Hardiman, B. S., Bohrer, G., Gough, C. M., Vogel, C. S., & Curtis, P. S. (2011). The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology*, 92(9), 1818–1827. <https://doi.org/10.1890/10.2192.1>
- Hardiman, B. S., Gough, C. M., Halperin, A., Hofmeister, K. L., Nave, L. E., Bohrer, G., & Curtis, P. S. (2013). Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. *Forest Ecology and Management*, 298, 111–119. <https://doi.org/10.1016/j.foreco.2013.02.031>
- Hibbs, D. E. (1983). Forty years of forest succession in Central New England. *Ecology*, 64(6), 1394–1401. <https://doi.org/10.2307/1937493>
- Hidding, B., Tremblay, J.-P., & Côté, S. D. (2013). A large herbivore triggers alternative successional trajectories in the boreal forest. *Ecology*, 94(12), 2852–2860. <https://doi.org/10.1890/12-2015.1>
- Horsley, S. B., Stout, S. L., & deCalesta, D. S. (2003). White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, 13(1), 98–118. [https://doi.org/10.1890/1051-0761\(2003\)013\[0098:WTDIOT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2)
- Ishii, H. T., Tanabe, S., & Hiura, T. (2004). Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science*, 50(3), 342–355.
- Kain, M., Battaglia, L., Royo, A., & Carson, W. P. (2011). Over-browsing in Pennsylvania creates a depauperate forest dominated by an understory tree: Results from a 60-year-old deer enclosure. *The Journal of the Torrey Botanical Society*, 138(3), 322–326. <https://doi.org/10.3159/TORREY-D-11-00018.1>
- Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19(4), 573–592. <https://doi.org/10.2307/1468118>
- Leibold, M. A. (1989). Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist*, 134(6), 922–949. <https://doi.org/10.1086/285022>
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69, 1–33. <https://doi.org/10.18637/jss.v069.i01>
- Lorimer, C. G. (1983). Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management*, 6(4), 343–360. [https://doi.org/10.1016/0378-1127\(83\)90042-7](https://doi.org/10.1016/0378-1127(83)90042-7)
- Miller, B. F., Campbell, T. A., Laseter, B. R., Ford, W. M., & Miller, K. V. (2009). White-tailed deer herbivory and timber harvesting rates: Implications for regeneration success. *Forest Ecology and Management*, 258(7), 1067–1072. <https://doi.org/10.1016/j.foreco.2009.05.025>
- Mori, A. S., Lertzman, K. P., & Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: A research agenda for applied forest ecology. *Journal of Applied Ecology*, 54(1), 12–27. <https://doi.org/10.1111/1365-2664.12669>
- Nuttle, T., Ristau, T. E., & Royo, A. A. (2014). Long-term biological legacies of herbivore density in a landscape-scale experiment: Forest understories reflect past deer density treatments for at least 20 years. *Journal of Ecology*, 102(1), 221–228. <https://doi.org/10.1111/1365-2745.12175>
- Nuttle, T., Yerger, E. H., Stoleson, S. H., & Ristau, T. E. (2011). Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere*, 2(1), art4. <https://doi.org/10.1890/ES10-00108.1>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlin, D., O'Hara, B., Minchin, P., Simpson, G., Solymos, P., Stevens, H., Szoecs, E., & Wagner, H. (2020). *The vegan Package* (2.5-7) [Computer software]. <https://CRAN.R-project.org/package=vegan>
- Parker, G. G., Harding, D. J., & Berger, M. L. (2004). A portable LIDAR system for rapid determination of forest canopy structure. *Journal of Applied Ecology*, 41(4), 755–767. <https://doi.org/10.1111/j.0021-8901.2004.00925.x>
- Patton, S. R., Russell, M. B., Windmuller-Campione, M. A., & Frelich, L. E. (2018). Quantifying impacts of white-tailed deer (*Odocoileus virginianus* Zimmerman) browse using forest inventory and socio-environmental datasets. *PLoS ONE*, 13(8), e0201334. <https://doi.org/10.1371/journal.pone.0201334>
- Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, 327, 251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>
- Ramirez, J. I., Jansen, P. A., & Poorter, L. (2018). Effects of wild ungulates on the regeneration, structure and functioning of



- temperate forests: A semi-quantitative review. *Forest Ecology and Management*, 424, 406–419. <https://doi.org/10.1016/j.foreco.2018.05.016>
- Reed, S. P., Royo, A. A., Fotis, A. T., Knight, K. S., Flower, C. E., & Curtis, P. S. (2021). Data for: The long-term impacts of deer herbivory in determining temperate forest stand and canopy structural complexity. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.b8gth7dn>
- Ritchie, J. C., Evans, D. L., Jacobs, D., Everitt, J. H., & Weltz, M. A. (1993). Measuring canopy structure with an airborne laser altimeter. *Transactions of the ASAE*, 36(4), 1235–1238. <https://doi.org/10.13031/2013.28456>
- Rooney, T., & Waller, D. (2003). Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management*, 181, 165–176. [https://doi.org/10.1016/S0378-1127\(03\)00130-0](https://doi.org/10.1016/S0378-1127(03)00130-0)
- Royo, A. A., & Carson, W. P. (2006). On the formation of dense understory layers in forests worldwide: Consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research*, 36(6), 1345–1362. <https://doi.org/10.1399/x06-025>
- Royo, A. A., Vickers, L. A., Long, R. P., Ristau, T. E., Stoleson, S. H., & Stout, S. L. (2021). The forest of unintended consequences: Anthropogenic actions trigger the rise and fall of black cherry. *BioScience*, 71(7), 683–696. <https://doi.org/10.1093/biosci/biab002>
- Russell, M. B., Woodall, C. W., Potter, K. M., Walters, B. F., Domke, G. M., & Oswalt, C. M. (2017). Interactions between white-tailed deer density and the composition of forest understories in the northern United States. *Forest Ecology and Management*, 384, 26–33. <https://doi.org/10.1016/j.foreco.2016.10.038>
- SAS Institute Inc. (2010). *SAS/STAT 9.1 user's guide (PROC GLIMMIX) [SAS]*. SAS Institute Inc.
- Seavy, N. E., Viers, J. H., & Wood, J. K. (2009). Riparian bird response to vegetation structure: A multiscale analysis using LiDAR measurements of canopy height. *Ecological Applications*, 19(7), 1848–1857. <https://doi.org/10.1890/08-1124.1>
- Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L., & Hicke, J. A. (2016). REVIEW: Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology*, 53(1), 120–129. <https://doi.org/10.1111/1365-2664.12511>
- Stromayer, K. A. K., & Warren, R. J. (1997). Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin*, 25(2), 227–234.
- Sullivan, F. B., Ducey, M. J., Orwig, D. A., Cook, B., & Palace, M. W. (2017). Comparison of lidar- and allometry-derived canopy height models in an eastern deciduous forest. *Forest Ecology and Management*, 406, 83–94. <https://doi.org/10.1016/j.foreco.2017.10.005>
- Tilghman, N. G. (1989). Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management*, 53(3), 524–532. <https://doi.org/10.2307/380972>
- Tremblay, J.-P., Huot, J., & Potvin, F. (2007). Density-related effects of deer browsing on the regeneration dynamics of boreal forests. *Journal of Applied Ecology*, 44(3), 552–562. <https://doi.org/10.1111/j.1365-2664.2007.01290.x>
- Ulyshen, M. D. (2011). Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. *Forest Ecology and Management*, 261(9), 1479–1489. <https://doi.org/10.1016/j.foreco.2011.01.033>
- Wales, S. B., Kreider, M. R., Atkins, J., Hulshof, C. M., Fahey, R. T., Nave, L. E., Nadelhoffer, K. J., & Gough, C. M. (2020). Stand age, disturbance history and the temporal stability of forest production. *Forest Ecology and Management*, 460. <https://doi.org/10.1016/j.foreco.2020.117865>
- Wang, Q., Pang, Y., Chen, D., Liang, X., & Lu, J. (2021). Lidar biomass index: A novel solution for tree-level biomass estimation using 3D crown information. *Forest Ecology and Management*, 499. <https://doi.org/10.1016/j.foreco.2021.119542>
- Weisberg, P. J., & Bugmann, H. (2003). Forest dynamics and ungulate herbivory: From leaf to landscape. *Forest Ecology and Management*, 181, 1–12. [https://doi.org/10.1016/S0378-1127\(03\)00123-3](https://doi.org/10.1016/S0378-1127(03)00123-3)
- White, M. A. (2012). Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest. *Forest Ecology and Management*, 269, 222–228. <https://doi.org/10.1016/j.foreco.2011.12.043>



#### Editor's Note

#### Threats to and Viability of Missouri's Natural Areas

In recent years, the concept of maintaining ecosystem resilience in an altered natural world has taken on greater significance in light of rapid environmental change. Efforts to improve biodiversity resilience in natural communities surrounded by urban and agricultural development and the ensuing disruption of ecological processes requires thoughtful, careful planning and implementation. One of the core concepts of resiliency of natural spaces involves size; larger natural zones tend to allow for greater ecosystem function (Biller, et al. 2009).

For the past 25 years or more, the Missouri Natural Areas Committee has embraced the concept that resilient ecosystems often require large-scale zones with buffer areas of similar landscape types. In recent years, for example, following a long history of restoration, the committee approved the expansion of the Coakley Hollow Fen NA from 5 acres to 1,773 acres to include the surrounding diverse woodlands and fens. Small, though intact high quality natural communities including small patches of railroad remnant prairies or sinkhole ponds, have great value in protecting and preserving biodiversity. However, they come with their own significant external threats. In the case of the railroad remnant prairies, one fast swipe of roadside herbicide can cause them to wink out forever.



**Image 1.** Lincoln Hills Natural Area (1,872 acres) in Cave River State Park (MDC, 4,400 ac.) encompasses a smaller natural area, Pickenswood Pond, a small sinkhole pond natural area designated in the 1980s. The natural area surrounding Pickenswood Pond expanded in 1988 to include the frequently burned and managed surrounding woodlands. Deer and exotic species management have occurred in the natural area and throughout the park for over 35 years. Urban encroachment at the park borders remains a viable threat, and staff work annually to continue management of this landscape scale natural area.

## MoNAC Newsletter Mailing List

To receive notification when new issues of the *Missouri Natural Areas Newsletter* are posted, e-mail [Michael.Leahy@mdc.mo.gov](mailto:Michael.Leahy@mdc.mo.gov).

This list-serve is *only* used to notify people of the link to the current natural areas newsletter web posting.

# Woodland Restoration is Truly Benefiting Birds in Missouri

by Frank R. Thompson

Birds capture the interest and enthusiasm of a wide segment of society that includes avid birdwatchers, backyard bird feeders, and upland game bird and waterfowl hunters. Birds are the focus of many conservation efforts led by federal and state governmental organizations and non-governmental organizations. There are great conservation success stories in North America, such as the recovery of the bald eagle and waterfowl populations. However, there are still many threats facing birds and overall, we have seen a 30% decline in the total number of birds in North America over the last 50 years. These declines have not affected all species equally. Some of the groups of birds with the most declining species are those that inhabit grasslands and scrub-successional habitats and species that are nocturnal insectivores.

Not coincidentally, these are groups of species that research and management has focused on in Missouri. A bright spot that has come out of research and management in Missouri is that if we restore and appropriately manage

natural communities, we can restore many bird species of concern to abundant levels in these communities and possibly bring back extirpated species. In other words, if we build it (or restore it), they will come.

Missouri's oak and pine savanna and woodlands declined precipitously in extent since European settlement and occur at less than 1% of their historic extent. The loss of these natural communities was due to extensive over-logging in the late 1800s and early 1900s, followed by decades of fire suppression and conversion to other land uses or succession to closed-canopy oak-hickory forests. Current declines in the abundance of many of the birds in the previously mentioned groups is likely linked to this loss of habitat. We have discovered that plant communities with open to mid-level canopy cover, a lack of midstory, and abundant ground cover consisting of a mix of grasses, forbs, and woody sprouts found in savanna and woodlands provides excellent habitat for many of these species. In fact, savanna and woodland habitat is import-

**Image 1.** Eastern Towhee (*Pipilo erythrophthalmus*) respond well to restoration efforts and key into a shrubby component associated with long-term fire management.



Photo by Melissa Roach



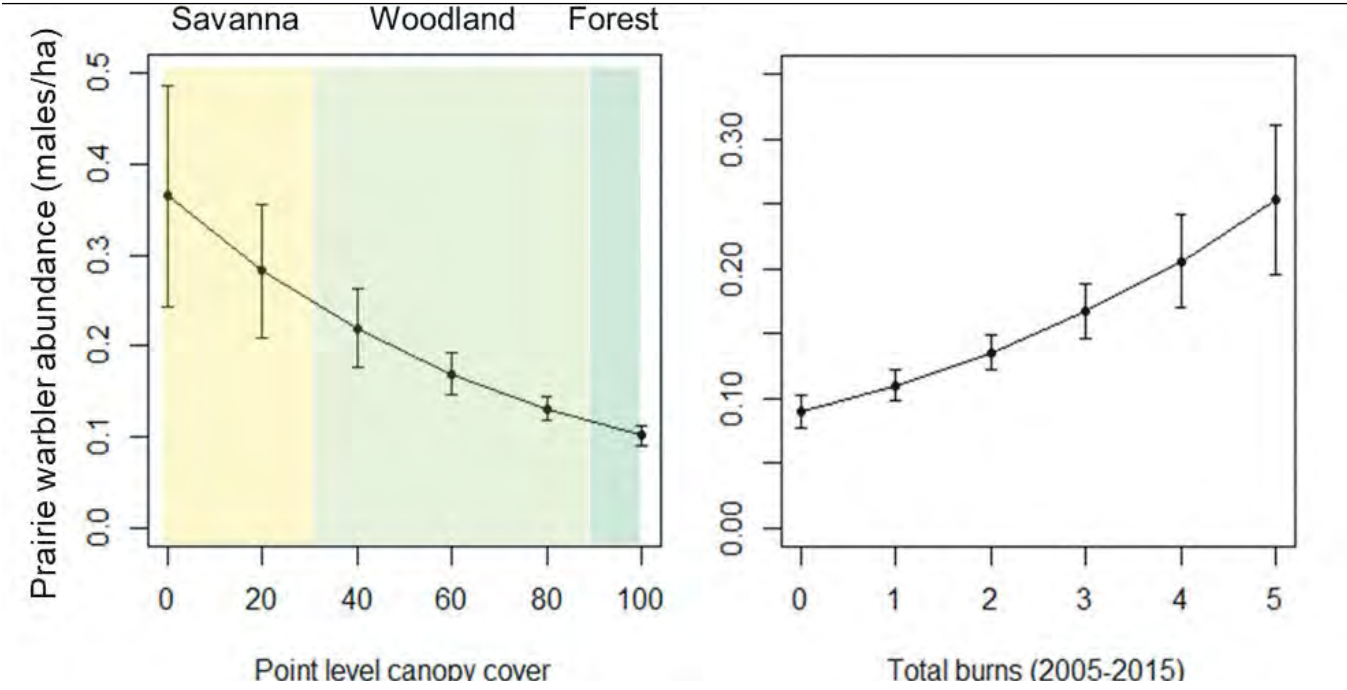
ant for 17 of the 29 most-threatened birds in Missouri according to the Missouri Bird Conservation Plan Technical Section (Table 1).

Conservation organizations in Missouri such as the Missouri Department of Conservation, Mark Twain National Forest, and Missouri Department of Natural Resources have been restoring and managing savanna and woodland for decades. However, efforts were greatly accelerated in 2012 with federal funding for pine woodland restoration on the Mark Twain National Forest under the Collaborative Forest Landscape Restoration program. We began monitoring bird response to oak savanna and woodland restoration in 2009 and then pine savanna and woodland restoration in 2013 and have documented a strong positive response by many of these species of concern. Open to mid-level canopy cover and periodic prescribed burning provides the abundant ground cover and patchy understory that many species nest and forage in, including Prairie Warbler, Yellow-breasted Chat, Blue-winged Warbler, and Eastern Towhee (Figure 1). Moderate canopy cover and tree densities also favor canopy-dwell-

Bachman’s Sparrow
Bewick’s Wren
Blue-winged Warbler
Brown Thrasher
Brown-headed Nuthatch
Chimney Swift
Chuck-will’s-widow
Eastern Towhee
Eastern Whip-poor-will
Eastern Wood-Pewee
Field Sparrow
Northern Bobwhite
Orchard Oriole
Prairie Warbler
Red-headed Woodpecker
Yellow-billed Cuckoo
Yellow-breasted Chat

**Table 1.** Most-threatened Missouri birds inhabiting savanna and woodland

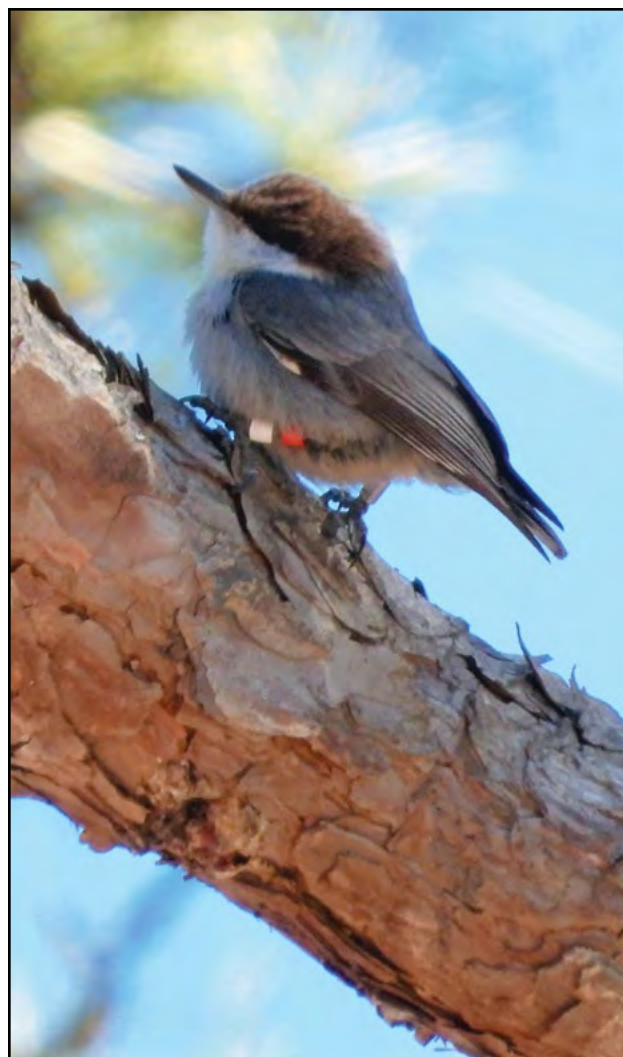
**Figure 1.** Across a range of savanna, woodlands, and forest in Missouri, prairie warblers reached their greatest abundance where overstory canopy cover was relatively open and there was periodic prescribed fire.



ing woodland species such as Red-headed Woodpecker and Eastern Wood-Pewee and nocturnal species such as Chuck-will's-widow and Eastern Whip-poor-will.

A particularly exciting aspect of these restoration efforts has been the translocation of the Brown-headed Nuthatch to Missouri pine woodlands (Image 2). The Brown-headed Nuthatch was last seen in Missouri in 1907 and may have been extirpated soon after due to the loss of pine woodlands. Conservation partners decided in 2019 that sufficient pine woodland had been restored to conduct an experimental translocation of nuthatches from Arkansas to Missouri pine woodlands. A total of 102 birds were moved in August and September of 2020 and 2021 and released on the Eleven Point Ranger District of Mark Twain National Forest. Post-release monitoring suggested that translocations efforts were successful in that no known mortalities or signs of stress occurred. However, birds moved more than expected and some dispersed from the release site. Some birds have successfully nested on the release area in each of the last three years but over the last three years the number of birds known to be alive on the release site has declined and partners are considering whether additional releases are needed to bolster the population. Investigators are currently analyzing survival and habitat use to try and identify factors affecting abundance. Nuthatches have very specialized needs for snags to excavate nesting cavities in, and one question that has been raised is there a sufficient snag density.

Our efforts studying breeding birds in the Ozark Highlands suggest several important considerations for sustaining their numbers in the region. We learned early on that minimizing forest fragmentation by non-forest land uses (i.e. development, agriculture) is important to ensuring productive populations. Savanna and woodland restoration through thinning and pre-



Missouri Department of Conservation file photo

**Image 2.** Brown-headed Nuthatch (*Sitta pusilla*) were reintroduced in the Missouri Ozarks and now inhabit pine woodlands that have undergone largescale restoration efforts on the Mark Twain National Forest.

scribed fire has also increased nesting success of the species that are dependent on these natural communities. While the group of species listed in Table 1 generally respond positively to restoration of savanna and woodland, they all have individual habitat requirements. This means to provide for all these species requires some diversity of habitat across the landscape, ranging from open savanna to closed woodlands in a matrix of forest structures and ages. In addition, species that nest and forage in the ground cover and understory have been found to respond to the number of years since the last fire depending on their pref-



ferences for more or less litter, grasses, forbs, and woody sprouts and shrubs. These needs can be met through different thinning targets and by having management units on staggered burn cycles. Alternatively, large landscape burns can create diversity in the groundcover, understory and overstory based on differences in fire behavior across different landforms.

I have studied the effects of forest management on birds over my entire career as a researcher. I have concluded that even-aged and uneven-aged forest management can benefit some of these disturbance-dependent birds of conservation concern while producing wood products and potentially income for landowners. Because of this both management objectives will continue to be important management tools. However, I believe the restoration of savanna and woodlands provides some unique conservation benefits for birds compared to these alternatives and the loss of these communities is probably a large part of why they are declining. I think the continued promotion of savanna and woodland restoration is important for bird conservation. 🦉

Frank R Thompson is Research Wildlife Biologist Emeritus, U. S. Forest Service and Adjunct Professor, University of Missouri  
Contact: [thompsonfr@missouri.edu](mailto:thompsonfr@missouri.edu)

References

Missouri Department of Conservation. 2019. Missouri Bird Conservation Plan Technical Section. Missouri Department of Conservation, Jefferson City, Missouri. <https://mdc.mo.gov/sites/default/files/2020-04/MOBirdConservationPlanTech.pdf>.

Reidy JL, FR Thompson, SW Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313, 34–46

Roach, Melissa C.; Thompson, Frank R.; Jones-Farrand, Todd. 2019. Effects of pine-oak woodland restoration on breeding bird densities in the Ozark-Ouachita Interior Highlands. *Forest Ecology and Management*. 437:443–459. <https://doi.org/10.1016/j.foreco.2018.12.057>.

Roach, MC, FR Thompson III, T Jones-Farrand. 2018. Songbird nest success is positively related to restoration of pine–oak savanna and woodland in the Ozark Highlands, Missouri, USA. *The Condor* 120: 543–556

Rosenberg, K, A Dokter, P Blancher, J Sauer, A Smith, P Smith, J Stanton, A Panjabi, L Helft, M Parr, P Marra. 2019. Decline of the North American avifauna. *Science*. 366. <https://doi.org/10.1126/science.aaw931>.

Thompson, F. R. III, M. C. Roach, and T. W. Bomnot. 2022. Woodland restoration and forest structure affect nightjar abundance in the Ozark Highlands. *Journal of Wildlife Management* 86:e2270. <https://doi.org/10.1002/jwmg.2270>

# 2024 Event Calendar

February 22–24, 2024

## Wetland Science Conference

Green Bay, Wisconsin  
[conference.wisconsinwetlands.org](https://conference.wisconsinwetlands.org)

March 1–2, 2024

## Conservation Federation of Missouri Annual Conference

Lodge of Four Seasons, Lake Ozark, MO  
[confedmo.org](https://confedmo.org)

March 25–29, 2024

## 2024 North American Wildlife and Natural Resources Conference

Amway Grand Plaza Hotel, Grand Rapids, MI  
[wildlifemanagement.institute/conference](https://wildlifemanagement.institute/conference)

April 9–11, 2024

## Missouri Grasslands Summit

Capitol Plaza Hotel, Jefferson City, MO.  
[confedmo.org/event/missouri-grasslands-summit](https://confedmo.org/event/missouri-grasslands-summit)

August 22–23, 2024

## Missouri Bird Conservation Initiative Conference

Columbia Country Club, Columbia Missouri  
[mobci.net](https://mobci.net)

Oct 7–10, 2024

## National Natural Areas Association Conference

Manhattan, Kansas  
[naturalareas.org](https://naturalareas.org)







# A Long Lesson in Resiliency: Ha Ha Tonka Karst Natural Area

by Allison J. Vaughn

The complex karst features, the rich surrounding terrestrial landscape, and the ruins of an early 20<sup>th</sup> century mansion led to the founding of Ha Ha Tonka State Park (HHTSP) in 1978, long after former governor Hadley proposed protection for the area's natural features in 1910. Shortly after the Missouri Department of Natural Resources (MDNR) acquired HHTSP, the Missouri Natural Areas Committee (MoNAC) nominated 70 acres of karst features and karst topography as a natural area in 1980. This 70 acres remains one of Missouri's outstanding geological areas, a classic example of a karst landscape (Image 1, previous page).

Interrelated solution features dramatically involved in this system include: an awe-inspiring cavern-collapse chasm bounded on the north by sheer cliffs nearly 250 ft. high and 800 ft. long, well-developed dry-mesic limestone forest, a long, deep-circulating spring (Missouri's 12<sup>th</sup> largest); two large sinkholes, a well-formed natural bridge, a moderately large cave (River Cave) with both sinkhole and swallet entrances, five smaller caves, and a losing stream (Dry Hollow) that courses through River Cave and ends in the spring. Notably, all of these significant karst features are located in a very small area, a true "microcosm" of a karst landscape. Today's Ha Ha Tonka Karst Natural Area was featured in *Geologic Wonders and Curiosities of Missouri* (Beveridge, 1980) and was proposed as a National Natural Landmark in the 1990s, 2002 and again in 2013. The NNL board disbanded shortly after the latest proposal was submitted

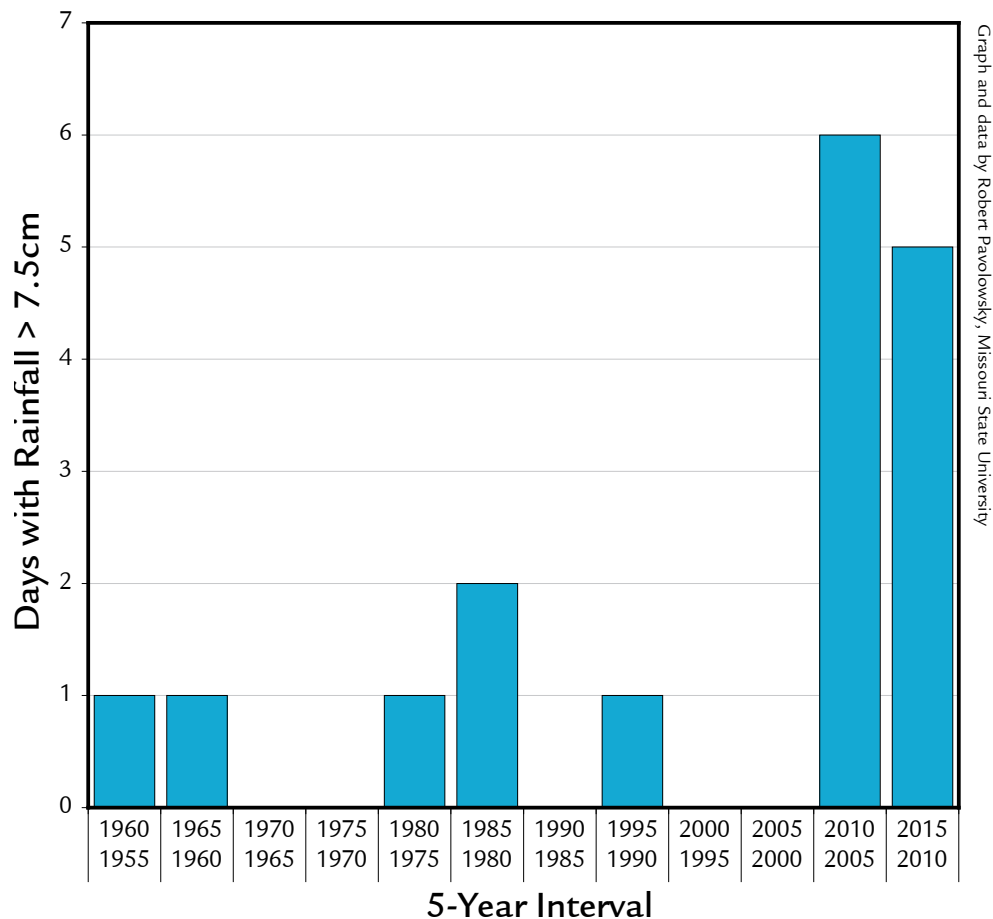
so the designation has never come to fruition.

In the 45 years since the creation of HHTSP, private domiciles—once few and far between in the immediate area—began surrounding the park, with landowners attracted to the landscape just like the early settlers were. However, since the mid-2000s, due to the park's proximity to Lake of the Ozarks, residential development adjacent to the park notably increased along a park conduit, Dry Hollow Road. This once-less traveled gravel road bisects a busy state highway and runs parallel to (and sometimes through) Dry Hollow, the losing stream that flows into River Cave. With the increased development along Dry Hollow Road, county road grading grew more frequent through time, with additions of creek gravel and fines on a regular basis to provide for smoother driving conditions. With each successive heavy rain event, gravel migrated from Dry Hollow Road, through the stream, into River Cave where ultimately, through a shallow underground conduit, it was deposited in Ha Ha Tonka Spring. The spring serves as a common outlet for approximately 100 mi.<sup>2</sup> of dry uplands to the south and east.

Beginning around 2003, during routine winter cave surveys of River Cave, park staff began recording gravel levels in the cave. Dry Hollow continued to fill with gravel not only from the surrounding watershed, but notably from the adjacent road. Since around 2013, with more frequent heavy rain events of short duration, gravel pulses coursing through the stream and through the cave (and ultimately the spring) continued apace.

---

**Image 1.** This 1979 aerial view of Ha Ha Tonka Spring represents the Ha Ha Tonka Karst Natural Area in the natural area nomination. In the late 1970s, the spring had not been prone to excess gravel accretion from the watershed and was fully open water throughout the spring run.



**Figure 1.** Graph illustrating days of rainfall higher than 7.5 cm (3 inches) that elevate to higher levels in the mid 2010s.

According to Pavlowsky, et al. (2016), high rainfall events occurred more frequently and with higher magnitude during the last decade compared to the 50 years prior (Figure 1):

For example, the 1% exceedance daily rainfall event has increased by 21% over the last decade (2005–2015) compared to the previous 20 years (1985–2005)...There were a total of 16 days with rainfall totals greater than 3 in. over the last 60 years (Figure 3B). However, these events were not evenly distributed over time. Daily rainfall totals only exceeded 3 in. six times from 1955–2005 (0.12 events/year), while exceeding that threshold ten times during the period from 2005 to 2015 (1 event/year) for a 8.3-times increase in frequency over the past decade.

One of those high rainfall events occurred at HHTSP July 1–2, 2015 in which 10 inches of rain fell in short duration, causing major flash flooding throughout the region. The event was so significant that Camden Co. declared a State of Emergency, triggering the Federal Emergency Management Administration to assess and repair the incurred damages to private and public property. In this event, approximately 300 cubic yards of ditch and road base material from Dry Hollow Road moved downstream through the culvert system and into the east entrance to River Cave, a secondary entrance protected by an angled iron gate to prevent trespass. As the cobble, road fines and larger sized gravel accumulated against the 7 ft. tall gate, the east sinkhole filled with water and overtopped the hillside separating the east entrance from the primary cave entrance in the



west sinkhole. The intensity of the flooding and whirlpool effect promulgated by the gate blockage resulted in a massive land slump in the west sinkhole which partially blocked the cave entrance and destroyed the 20 ft. tall primary chute gate built to allow for bat passage. The land slump left large boulders, gravel, and soil in front of the primary passage, thereby altering the airflow into the cave (Image 2). River Cave is home to a significant maternity colony of endangered gray bats, estimated at 150,000.

Shortly after the rain event, MDNR hydrologists, engineers, and Missouri Geological Survey (MGS) staff assessed the damage and provided a strategy to mitigate continued gravel input in the cave. In an unpublished MGS report, it was recommended to culvert the road out of the stream bed, and for park staff to seek permission to remove gravel following heavy rain events from the stretch of the stream on park property above the east entrance to River Cave. Included in the report was a recommendation to ultimately seek funding to pave Dry Hollow Road and dredge gravel out of Ha Ha Tonka Spring. The immediate work ahead involved a FEMA contract utilizing cranes and bulldozers to remove debris and the 20 ft. tall damaged cave gate, which consisted of several tons of steel, from the primary sinkhole entrance to River Cave (Image 3). This costly endeavor resulted in park staff and volunteers tackling the debris in the east sinkhole by hand with buckets. The FEMA contract also funded the cave gate replacement that was built by park staff and Americorps-St. Louis.

By 2016, gravel in River Cave increased to the level that entry into the secondary 7 foot tall east entrance (which historically housed wintering Indiana bats) required crawling to enter. Interstitial spaces continued to fill with road fines, and gravel blocked some smaller cave passages. Together, this negatively impacted River Cave's invertebrate and salamander populations.

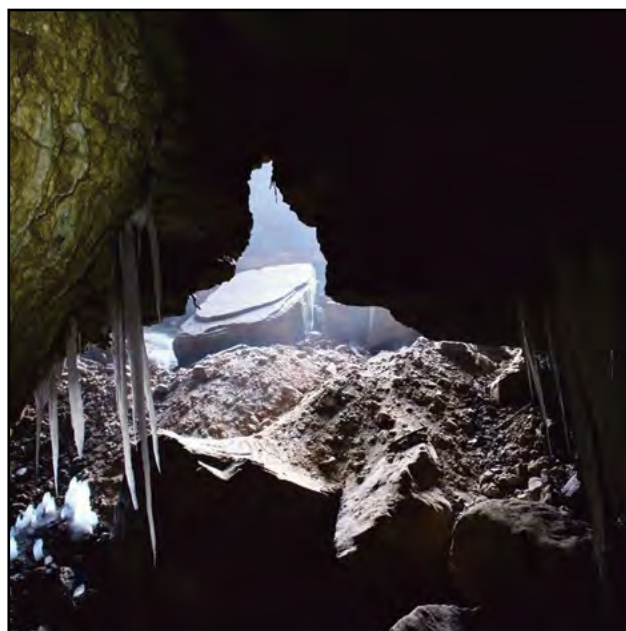


Photo by Allison Vaughn, Missouri Department of Natural Resources

**Image 2.** The left side of the main River Cave entrance in the winter after the debris collapse in July essentially blocked air flow and passage with boulders and gravel fines. A large section of the entrance was cleared of debris in August, 2015, but some still remains.



Photo by Allison Vaughn, Missouri Department of Natural Resources

**Image 3.** After the debris from the flood event was removed, contractors also removed tons of steel from the chute cave gate, revealing the natural entrance to River Cave. The cave gate was replaced the same week to prevent trespass. The wooden steps leading into the sinkhole remain out of commission in 2024 due to instability of the hillside in which the steps are anchored.





Photo by Allison Vaughn, Missouri Department of Natural Resources

**Image 4.** Gravel islands formed quickly in Ha Ha Tonka Spring as this photo from 2016 illustrates. By 2020, the islands were vegetated with roadside vegetation, including tall fescue.

The sump at the back of River Cave continued to clog with gravel as it coursed its way through the cave, with hydrostatic pressure ultimately forcing the gravel through the underground conduit and into the spring. Spring discharge is strong enough to move large amounts of gravel. However, through time, improvements to Dry Hollow Road and regular gravel removal from the stream slowly began to lessen the gravel input in the cave, but there remained much in the cave system. By summer 2016, large gravel islands with roadside vegetation began to develop in the spring (Images 4 and 5).

In 2019, in collaboration with MDNR, the Camden County Road Commission sought grant funding to allow for the paving of a one mile stretch of Dry Hollow Road that runs adjacent to the stream. They secured a Community Block Grant from the State of Missouri, but work could not begin immediately. However, the gravel road improvements and continued removal of gravel from the stream significantly



Photo by Allison Vaughn, Missouri Department of Natural Resources

**Image 5.** By August 2023 two months after the dredging project ended, native spring vegetation had recolonized the spring.



lessened the input into the cave. By 2021, winter cave surveys revealed much less gravel, as it was coursing through the karst system, and wildlife populations began to rebound in the cave; for example, the rimstone pools that house grotto salamanders were free of gravel for the first time in several years. In Ha Ha Tonka Spring, however, gravel islands increased in size to the degree that they blocked water flow from parts of the spring branch, resulting in stagnant isolated shallow pools scattered throughout the lower reaches of the spring. Native spring vegetation began to diminish, with the large stands of bur reed and watercress slowly disappearing. The spring was slowly filling with gravel.

Botanist Julian Steyermark catalogued the flora of multiple freshwater springs in Missouri, including Ha Ha Tonka Spring, creating comprehensive plant lists and spring descriptions in his article *Phanerogamic Flora of Freshwater Springs in the Ozarks of Missouri* (1940). He described Ha Ha Tonka Spring as a vegetated spring, with notable spring species in abundance:

At the very beginning, in deep water, are large beds of milfoil, alternating with water cress. Along the sides are rocks covered with algae and mosses. ... All along the margin and in the center of the basin are long strands of water milfoil (*Myriophyllum heterophyllum*), and along the deeper portions of the margin grow plants of hornwort (*Ceratophyllum demersum*). These two species are the only ones found in the basin. The right spring branch runs along the base of a precipitous, rocky wall and is deep. The only plants which occur in it are hornwort, milfoil, and occasionally water cress (*Nasturtium nasturtium-aquaticum*). The left spring branch is very rich in aquatic plants. It is narrow, about 10 to 12 feet wide, and has a deep blue-gray color. Here are beds of broad-leaved, purple or green

mild water pepper (*Polygonum hydropiperoides*), bur reed (*Sparganium americanum*), water starwort (*Callitriche heterophylla*), and water speedwell (*Veronica concatenata*), the last very abundant. Mild water pepper grows where the current is fastest, while bur-reed occurs mostly along the margin of the branch. The spring empties into the Niangua River about a half-mile away from its source. (p. 162)

In late 2022, after much planning and securing of additional grant funds, Camden County paved the one mile stretch of Dry Hollow Road that was impacting the stream. By this time, River Cave and Dry Hollow Stream possessed far less gravel than in previous years, and with the paving of the road, the gravel input is now slated to come only from the stream and surrounding watershed. The next activity was to secure funding for the dredging of the spring. Understanding the significance of this natural feature in the park, MDNR funded the dredging through the Fiscal Year 2024 Capital Improvement Budget. Research into this project involved using late 1970s reports from then-Division of Geology and Land Survey's (now MGS) renowned hydrologist Jerry Vineyard, his landmark book *Springs of Missouri* (1982) and images of the spring from Steyermark's 1940 publication. MDNR staff collaborated with engineers and spring experts to determine the historic depth of the spring. Permitting and planning required significant effort from both MDNR and the engineering firm, but in summer 2023, the two months-long dredging project concluded in early June with the final total removal of 10,565 cubic yards of gravel and road fines. The isolated gravel islands that had formed from the deposition of gravel from River Cave over eight or more years were removed.

To undertake this project, terrestrial vegetation typical of a dry-mesic limestone forest along

the lower Spring Trail was negatively impacted to allow passage for dredging equipment. Efforts were made to prevent erosion after the operation was complete, and it is hoped that through time, the herbaceous vegetation will recover. To conduct the gravel dredging, contractors created a wide passage along the Spring Trail at the base of the forest, and a gravel road into the heart of the spring pool for the equipment to reach the gravel islands slated for removal. Notably, by August 2023, spring vegetation, including mats of watercress at the bottom of the spring, bur-reed, water milfoil, hornwort, water speedwell, and water starwort began to repopulate the spring and spring branch (Image 6).

The 8-year long process to complete the action items set forth in the MGS report following the July 2015 rain event required many moving parts and partners. Ha Ha Tonka SP has always been a stable and resilient landscape. With development and other threats occurring at the park's borders,

park managers recognize the importance of monitoring these threats that come part and parcel with land management in the 21st century. The vegetative response in Ha Ha Tonka Spring and the surrounding Ha Ha Tonka Karst NA following such dramatic alterations, the wild-life response in River Cave and the spring, will hopefully continue to improve to continue the park's legacy of serving as a gem in the crown of Missouri state parks. 🌿

---

**Allison J. Vaughn** is a Natural Resource Ecologist with the Missouri Department of Natural Resources.

Contact: [allison.vaughn@dnr.mo.gov](mailto:allison.vaughn@dnr.mo.gov)

#### References

- Pavlovsky, Robert T. Ph.D., Marc R. Owen, M.S., and Rachael A. Bradley.** "Recent increase in extreme rainfall amounts in the Big Barren Creek Watershed, S.E. Missouri." *Missouri Natural Areas Newsletter*. Volume 16 Number 1, 2016. Pp 19–24.
- Beveridge, Thomas R.** *Geologic Wonders and Curiosities of Missouri*. Missouri Department of Natural Resources, Division of Geology and Land Survey. 1978. (Vineyard, Jerry D., revised edition 1990). Pp. 208–283.
- Vineyard, Jerry o., and Gerald L. Feder.** 1974, *Springs of Missouri*: Mo. Geological Survey and Water Resources, WR 29, 212 p., 94 figs., 26 tbls. Revised edition (1982).
- Steyermark, Julian.** 1940. Natural plant associations and succession in the Ozarks of Missouri. II. Phanerogamic flora of the fresh-water springs in the Ozarks of Missouri. *Fieldiana. Botany* series v. 9, no. 6, pt. 2.

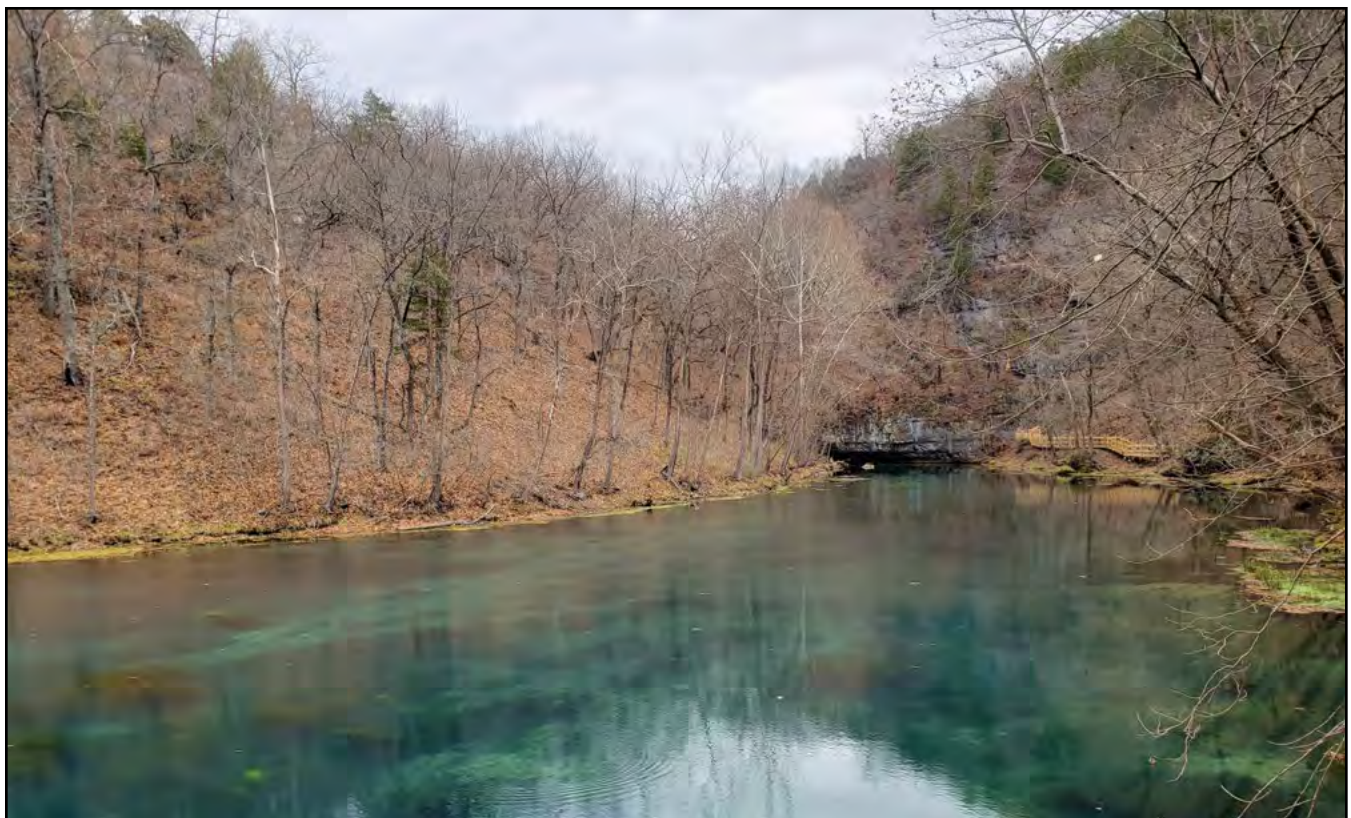


Photo by Allison Vaughn, Missouri Department of Natural Resources

**Image 6.** Ha Ha Tonka Spring in November, 2023 after the native spring vegetation went dormant.